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Movements of Mountain Whitefish (*Prosopium williamsoni*) in the Sheep River Watershed, Alberta

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DAVIES, R. W., AND G. W. THOMPSON. 1976. Movements of mountain whitefish (*Prosopium williamsoni*) in the Sheep River watershed, Alberta. J. Fish. Res. Board Can. 33: 2395–2401.

Movements of mountain whitefish (*Prosopium williamsoni*) in the Sheep River were studied during 1972 and 1973. Movement patterns of young-of-the-year and immature whitefish are ill-defined. Although some adult mountain whitefish are nonmigratory, the majority are migratory and show complex movement patterns including spring feeding, summer feeding, prespawning, spawning, and postspawning-overwintering movements. Environmental factors affecting and/or controlling these movements are discussed.

DAVIES, R. W., AND G. W. THOMPSON. 1976. Movements of mountain whitefish (*Prosopium williamsoni*) in the Sheep River watershed, Alberta. J. Fish. Res. Board Can. 33: 2395–2401.

Nous avons étudié les déplacements du ménomini des montagnes (*Prosopium williamsoni*) dans la rivière Sheep en 1972 et 1973. Les déplacements des jeunes de l'année et des immatures sont mal définis. Bien que quelques ménominis des montagnes ne soient pas migrateurs, la majorité le sont et montrent un ensemble de mouvements compliqué, y compris migrations d'alimentation de printemps, d'alimentation d'été, d'avant la fraie, de fraie et d'après la fraie-hivernage. Nous analysons les facteurs de l'environnement affectant et/ou contrôlant ces déplacements.

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MOUNTAIN whitefish (*Prosopium williamsoni*) occur in most east-slope streams of Alberta (Paetz and Nelson 1970) and are becoming increasingly important as a game species (Thompson 1970). Observations on the age, growth, reproduction, and feeding of mountain whitefish have been reported by Thompson and Davies (1976) but relatively little is known about the seasonal timing and other aspects of their movements. This paper describes the movements of mountain whitefish within the Sheep River watershed, Alberta and considers the mechanisms initiating, orienting, and controlling the process.

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Materials and Methods

The study area included the entire Sheep River watershed although most of the work was concentrated in a 12-km section of the upper Sheep River (Fig. 1) from George Creek to the Sandy McNab Campground (60 km southwest of Calgary, Alberta). A description of the watershed area including a physical, chemical, and biological description of the Sheep River is given in Thompson (1974).

Movements of young-of-the-year and some 1-yr-old whitefish were assessed during 1972 and 1973 by regular sampling with seines and electrofishers at the seven sites and four regions identified on Fig. 1. The number and size of the whitefish collected from each site were recorded.

Movements of 1-yr-old and older whitefish were assessed using three types of tags: numbered Petersen button tags, numbered Floy spaghetti dart tags, and numbered, colored Floy T flag tags.

Active whitefish were observed to lose their scales readily upon handling, so MS-222® (ethyl *m*-aminobenzoate methanesulfonate) was used to anesthetize them. Between 30 and 40 ppm anesthetized the fish within 1 min, caused no mortality, and in most instances eliminated scale loss.

Tags were recovered in two ways. A reward of $1.00 was offered by the Alberta Department of Recreation, Parks and Wildlife, Fish and Wildlife Division, for the return of tags by anglers together with the appropriate information. Movements of whitefish were also assessed by periodically sampling with fish traps, seines, electrofishers, and primacord in the Sheep River and Ware Creek. Additionally, the Sheep River from the Sheep River Falls to Turner Valley was swum with the aid of snorkel, fins, and mask almost once a week from the end of June until the first of November, 1973.

Results

Hatching and emergence begins in April and continues to the middle of May followed by an immediate downstream dispersal (Thompson and Davies 1976). Whitefish fry were collected in the shallow backwaters (5–20 cm deep) of the lower Sheep River (Turner Valley downstream) in June, July, and August (Fig. 2) but were found in only two backwaters above Turner Valley (High Noon Ranch and Kroeker Construction). Laboratory observations of newly hatched fry indicated they could not swim against a water velocity in excess of a few centimeters per second.

Prior to attaining a fork length of 55 mm, whitefish were obtained from low velocity areas with a substrate of gravel, sand, or mud. However, upon reaching 55–60 mm in mid-to-late August, whitefish move to the fringes and tail end of pools where there is a noticeable increase in water velocity and a substrate of rock and rubble.

From late September to early November, large schools (in excess of 2000) of young-of-the-year whitefish (mean length of 99.7 mm ± 2.8, 95% confidence limits) were observed immediately below an impassible weir across the Sheep River at Turner Valley. As resident young-of-the-year whitefish were 79.8 mm ± 3.2 (95% confidence limits) in fork length (Thompson and Davies 1976), it was evident these larger young-of-the-year whitefish had moved upstream but were unable to get above the weir. In early November all young-of-the-year whitefish dispersed downstream.

Limited data are available on the movements of 1-yr-old whitefish. Figure 3 shows that numerous 1-yr-old whitefish were collected in October only at the weir in Turner Valley. In December and February, 1-yr-old-whitefish were collected (some tagged and released) in shallow (18–30 cm deep), iced-over backwaters in the Highwood and Bow rivers. To date, none of these tagged whitefish have been recaptured.

On June 13, 1972 a weir was constructed on Pekisko Creek, a small tributary to the Highwood

FIG. 1. Study area with sampling locations (■) and regions A, B, C, and D.

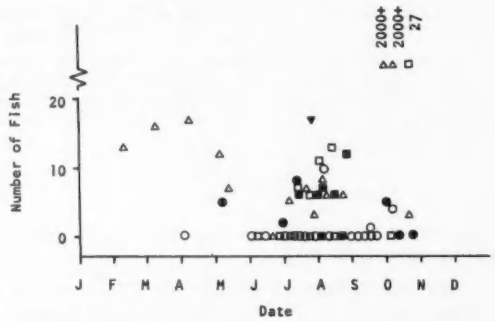

FIG. 2. Locations and numbers of 0-yr-old *Prosopium williamsoni* captured in the Sheep River in 1973: Okotoks (●), Turner Valley (△), High Noon Ranch (□), Sandy McNab Campground (○), Kroeker Construction (■), and Bow River at Carseland (▼).

TABLE 1. Adult *Prosopium williamsoni* tagged in late August 1973, with distance of downstream movement prior to spawning indicated.

Date tagged	No. tagged	Location tagged	Date tag returned	No. of tags returned	Distance moved (*km*)	
					Avg	Range
Aug. 27, 1973	44	A	Sept. 18, 1973	13	8.3	2.7–10.3
Aug. 28, 1973	29	B	Oct. 4, 1973	1	11.7	0–31.4
			Sept. 18, 1973	6		
			Sept. 27, 1973	1		
Aug. 28, 1973	17	C	Aug. 29, 1973	1	17.1	5.1–29.0
			Oct. 4, 1973	1		
Aug. 29, 1973	52	D	Sept. 15, 1973	5	7.4	2.6–26.4

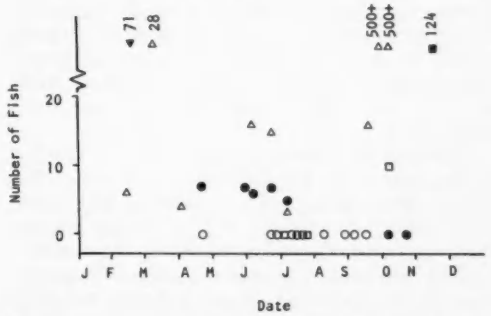

FIG. 3. Locations and numbers of 1-yr-old *Prosopium williamsoni* captured in the Sheep River in 1973: Okotoks (●), Turner Valley (△), High Noon Ranch (□), Sandy McNab Campground (○), Highwood River at Mouth (■), and Bow River at Carseland (▼).

River. On nine occasions from June 15 to July 11, 1972 up to 200 whitefish were observed above the weir. The weir had apparently delayed their downstream movement. On 3 days each year in May and June of 1972, 1973, and 1974 whitefish were electrofished from Ware Creek. Subsequent electrofishing on 3 days in late July and August of the same years showed the whitefish were absent.

On April 25 and 26, 1973 the Sheep River (not yet completely free of ice) from Gorge Creek to Sandy McNab Campground was electrofished with a boat shocker. Only 11 adult whitefish (3 yr old and older) were captured and tagged; 2 were recaptured on September 18 and 1 on October 21, 1973 in exactly the same pool. Seven adult whitefish were collected from the same region during November.

Using a wet suit and snorkel, no whitefish were observed in the Sheep River from Gorge Creek to Sandy McNab Campground on July 6, but on July 19, 1973 in excess of 700 adult whitefish were observed in the same stretch of river, indicating a large upstream movement had occurred during the interim. While snorkeling during the latter part of July, all of August, and the first part of September, we observed whitefish from Gorge Creek to Turner Valley in most pools deeper than 1 m, in concentrations of 3–50 fish per pool. From August 27 to 29, a total of 142 whitefish were caught, tagged, and released in pools between Gorge Creek and Sandy McNab.

Between September 15 and 17, 1973, whitefish concentrated in large numbers (approximately 30–200) in a few deep pools (2 m deep or more) in the upper Sheep River. Tag returns (Table 1) showed whitefish from upstream areas had moved downstream an average distance of 10.1 km to congregate in these large pools. A similar downstream movement occurred on September 13 and 15, 1972 when approximately 200 and 400 whitefish were captured in a two-way trap while moving downstream past Sandy McNab Campground.

On September 27, 1973 a definite movement of mature whitefish occurred. This was shown by subsequent tag returns to be a downstream movement averaging 27 km. Snorkeling in the upper Sheep River from September 28 to November 1, 1973 showed very few whitefish present.

From October 3 to 10, 1973 up to 700 whitefish were observed in a pool immediately above the weir at Turner Valley (Fig. 4), of which 18 had been tagged with colour-coded T tags. These fish were tagged at the end of August between Gorge Creek and Sandy McNab indicating, a fall downstream movement of whitefish.

While 63 whitefish were tagged in region A in September 1972, only 10 were recaptured in regions A, C, or D within the following 7–12 mo, 4 were recaptured at Sandy McNab within 10–12 mo, and 1 was recaptured at Turner Valley after 1 mo and another after 13 mo. Of 60 whitefish tagged in November 1972 at Okotoks, 6 were recaptured in the same location: 3 within

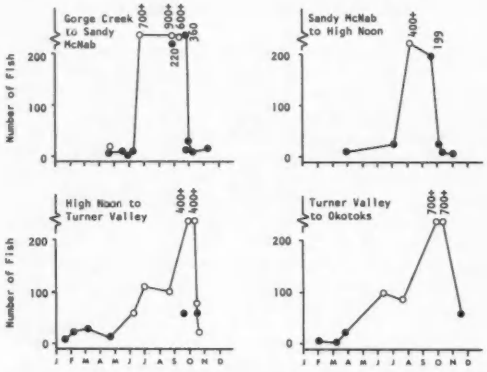

FIG. 4. Adult *Prosopium williamsoni* populations in various sections of the Sheep River as indicated by the number of whitefish collected (●) and/or observed (○).

3 wk, 2 within 5 mo, and 1 almost a year later. Of 11 whitefish tagged in the upper Sheep River in April 1973, 2 were recaptured in the same location in September and 1 in October, of the same year.

Upon completion of spawning, usually by the 2nd wk of October, a further downstream movement to lower stretches of the Sheep River and even the lower Highwood and Bow rivers occurs where the whitefish overwinter in shallow backwaters (Fig. 4). On four occasions from November to March of 1972–73, whitefish were tagged in shallow backwaters (<30 cm deep) in the lower Sheep and Highwood rivers and the Bow River but none of these whitefish have been recaptured.

Discussion

Movement of Young Whitefish

Upon emergence, fry drift passively downstream until suitable holding areas are encountered. Considerable effort was expended in the search for whitefish fry upstream of Turner Valley, but few were obtained. This downstream movement has not been quantified but the lack of suitable holding areas (shallow backwaters) in the upper Sheep River, the small size of the fish upon hatching (Thompson and Davies 1976), the weak swimming ability of newly hatched fry, and water velocities which exceed 1 $m \cdot s^{-1}$ in the spring, all support a passive downstream movement.

Downstream of Turner Valley the Sheep River becomes a braided channel offering many suitable habitats for whitefish fry. Numerous fry were seined from the lower Sheep River in shallow backwaters (usually <25 cm deep) with no measurable water velocity. Brown (1952), and Pettit and Wallace (1975) found many young-of-the-year whitefish in a similar habitat in their studies.

Young-of-the-year whitefish show strong positive phototaxis (Liebelt 1970) which may relate to their selection of shallow, exposed backwaters, and stream margins. This habitat is not normally occupied by the other indigenous salmonids in the Sheep River.

Whitefish fry were usually collected in groups of three or less which may be a behavioral trait to decrease predation. Ware (1973) suggests the probability of prey discovery is determined by the predator's ability to distinguish targets against a background. The shape and distribution of parr marks on fingerling whitefish did not contrast sharply with the rest of their body and they blended well with the pea-size gravel in their habitat.

Schooling of whitefish became evident in September when the fish reached 65–80 mm fork length. This agrees with Nelson (1962) who found whitefish schooling at 7 mo of age in the Kananaskis River and Barrier Reservoir. Schooling may be associated with an upstream movement of young-of-the-year and 1-yr-old whitefish in early October. These two year-classes of whitefish were observed for almost a month in the spillway tailrace of the weir at Turner Valley before redispersing downstream. The weir is washed away each spring during runoff and repaired every August or September when Sheep River flows drop. Upstream movements are therefore not restricted from April through late August or early September, but is restricted at all other times. Downstream movements appear to be temporarily delayed by the weir but fish can move downstream by utilizing a metal spillway.

The upstream movement of young-of-the-year and 1-yr-old whitefish to Turner Valley coincides with the downstream movement of adult whitefish. This may be a behavioral response to avoid predation and/or competition between the two groups.

The overwintering location of young-of-the-year and 1-yr-old whitefish is not well defined but it seems probable that they overwinter in shallow backwaters or the shallows along the river margins or pools of the lower Sheep River and the Highwood and/or Bow rivers.

Movement of Adult and Subadult Whitefish

The location of a few 2-yr-old whitefish appears to be similar to older (hereafter referred to as adult) whitefish. The data suggest that a few

immature 2-yr-old whitefish accompany adult fish throughout the spring and summer, but as the spawning season approaches, the immature fish either move downstream with or in advance of the adults.

The 3-yr-old age-classes of whitefish were abundant in the Sheep River from 1972 to 1974, while during the same time, the 2-yr-old age-class was virtually absent. Numerous 2-yr-old whitefish were sampled near the mouth of the Highwood River and at the Carseland Weir in 1972 and 1973. It is speculated that the majority of 2-yr-old whitefish are in the Highwood and Bow rivers and return to the Sheep River when they mature.

Migrant vs. nonmigrant — Most whitefish in the Sheep River undertake extensive movements in their adult lives, although a small segment appears to remain within the upper Sheep River. This assumption is based on the collection of a few adult whitefish in the upper Sheep River prior to the detection of any upstream movement and the collection of low numbers of adult whitefish when the determined downstream movement of the majority of the population had been completed.

There are selective advantages to migrant and nonmigrant forms. It is hypothesized that the migrant whitefish can utilize the higher secondary production in the downstream areas and therefore can become much larger or grow faster. The disadvantage of being migrant is that the fish are potentially exposed to a greater number of hazards that might increase mortality. The nonmigrant whitefish are able to make maximum use of the available remaining resources once the migrant whitefish are gone. The advantage of having migrant and nonmigrant forms in the population is a potentially greater gene pool diversity.

The majority of adults are migratory in nature and the following data and suggestions are offered, in speculation, as to the type of mechanisms involved in the timing and periodicity of these migrations.

Spring-feeding movements — Electrofishing and snorkeling have shown that few whitefish were present in the Sheep River prior to the middle of July 1973. Observations of Pekisko and Ware creeks suggests numerous adult whitefish were present in the creeks during May, June, and early July. After mid-July, whitefish were absent from both creeks indicating that the whitefish had moved down and out of these small tributaries.

Erickson (1966) indicated that some whitefish migrated out of the Snake River, Utah, and into tributary streams during the spring and summer. He attributed the migrations to a feeding pattern that was closely associated with increasing water temperatures and volumes in the tributary streams. It seems likely that some whitefish move out of the Sheep River and into tributary streams during the spring to feed for similar reasons.

Spring-feeding migrations and their importance should not be disregarded. Most salmonids, including whitefish, are visual feeders. Clearly, it would be advantageous to the whitefish to move into feeding areas where they can see their food if turbidities in the Sheep River prevent efficient utilization of the food resources there. The availability of prey species in Ware Creek in the spring was evident from whitefish stomach samples (Thompson and Davies 1976).

As Sheep River physical data were incomplete, it was necessary to use data collected by Water Survey of Canada on the Highwood River to show the relationships of temperature, turbidity, and streamflow of the Sheep River and Ware Creek. The data are comparable, because the Sheep and Highwood rivers drain the first and second mountain ranges from the foothills and therefore have similar flows and turbidities. Ware Creek only drains the front range. Isohyetal maps (Poliquin and Hanson 1973) show the mean winter precipitation for the front range is low (<25 cm) while the mean winter precipitation for the second range is moderate (25–50 cm) to high (50–75 cm). The physiography of the mountains plus the winter precipitation have a tendancy to create the spring runoff from the front range approximately 4–6 wk in advance of the second range.

Turbidity and stream flow in Ware Creek starts decreasing in mid-May with a subsequent steady increase in water temperature. Conversely, Sheep River turbidities and streamflows increase in mid-May with no increase in temperature. Some whitefish move into small tributaries of the front range (e.g. Ware Creek) and take advantage of the food supply. As temperatures continue to rise, stream discharge and level decrease drastically in mid-to-late June, causing the whitefish to move out of the front range tributaries and into the larger rivers where conditions had become suitable for feeding. This ensures successful exploitation of food sources made available at different times and in different locations.

Summer-feeding movements — Adult whitefish moved into the upper Sheep River sometime during the 2nd wk of July, 1973. The time lag of approximately 6 wk for physical conditions to improve in the Sheep River as compared to Ware Creek, correlated with the later growth and

emergence patterns of stream invertebrates in the upper Sheep River area (Hartland-Rowe 1964) suggests that the stimulus for upstream spring and summer movements may be similar.

Spawning movements — Between September 13 and 17, 1973 whitefish vacated most pools, moved downstream approximately 10 km, and congregated in large numbers in a few deep (2 m or more) pools. This prespawning movement corresponded with a drop in the minimum daily water temperature from 6 to 2 C during the 4-day period (Thompson 1974). Bringing these fish together at this time increases the probability of successful reproduction.

On September 27 these pools were vacated and the whitefish moved downstream. This movement began during the day. There appeared to be no significant change in water temperature associated with this movement. Analysis of this second movement showed it to be closely associated with spawning.

Once spawning is completed, the whitefish continue downstream (postspawning movement) but neither the distances nor exact locations have been quantified. The distances are considerable because after October 10, only 11 whitefish were observed in the upper Sheep River and spawning had been documented as far upstream as Sandy McNab Campground (Thompson and Davies 1976).

Observations suggest this postspawning movement is to the lower reaches of the Sheep River and possibly into the Highwood and Bow rivers. The Sheep River is subject to low winter flows and this postspawning movement is probably a movement to suitable wintering areas. On November 29, 1973 numerous whitefish were observed in a pool at Okotoks. On February 4, 1974 the pool was empty. Clearly the whitefish undertake some winter movements but their nature is unknown. Pettit and Wallace (1975) suggest that after spawning, the whitefish of Kelly Creek, Idaho, migrate downstream and overwinter in the deeper pools where winter conditions are less severe.

Movements of whitefish within the Sheep River are complex. The foregoing is solely a descriptive account of periodicity, direction, magnitude, and locality of these movements with suggestions offered as to mechanisms initiating, orienting, and controlling them. These movements profoundly influence the availability of whitefish for capture by man and management regulations must be set accordingly. Figure 5 is a diagrammatic representation of the movements of adult Sheep River whitefish with suggested related and/or controlling factors.

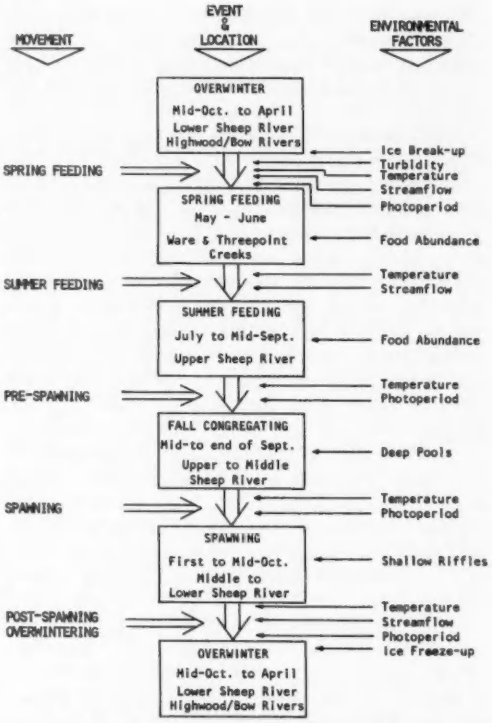

FIG. 5. Diagrammatic representation of the movements of adult *Prosopium williamsoni* in the Sheep River with suggested related and controlling factors.

Acknowledgments

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Performance of Lake Trout (*Salvelinus namaycush*) Backcrosses, F_1 Splake (*S. fontinalis* × *S. namaycush*), and Lake Trout in Lake Huron[1]

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SPANGLER, G. R., AND A. H. BERST. 1976. Performance of lake trout (*Salvelinus namaycush*) backcrosses, F_1 splake (*S. fontinalis* × *S. namaycush*), and lake trout in Lake Huron. J. Fish. Res. Board Can. 33: 2402–2407.

This paper presents the results of plantings in Lake Huron waters of lake trout (*Salvelinus namaycush*), F_1 splake (*S. fontinalis* × *S. namaycush*), and the progeny of the backcross between splake males and lake trout females.

The planted fish were piscivorous throughout age-groups II – V with rainbow smelt (*Osmerus mordax*), sticklebacks (*Pungitius* [?]), and alewives (*Alosa pseudoharengus*) the dominant food organisms. Hybrid stocks grew more rapidly but attained a somewhat smaller asymptotic length than did lake trout. The F_1 hybrids were the earliest to mature with 34% of the males and 4% of the females spawning at age II. Earliest maturity occurred in the backcrosses at age III, in contrast to lake trout which matured predominantly at ages VI and VII. The backcrosses demonstrated a slightly broader thermal and bathymetric distribution during summer than did lake trout, while the F_1 hybrids tended to concentrate in the thermocline. Total annual mortality rates (attributed mostly to predation by sea lampreys, *Petromyzon marinus*) ranged from 62 to 95% for all of the planted stocks.

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Le présent article décrit les résultats d'implantations, dans les eaux du lac Huron, de touladis (*Salvelinus namaycush*), de truites moulac de F_1 (omble de fontaine (*S. fontinalis*) × touladi) et de descendants de rétrocroisements entre des truites moulac mâles et des touladis femelles.

Les poissons implantés sont piscivores entre les âges II et V, l'éperlan arc-en-ciel (*Osmerus mordax*), les épinoches (*Pungitius*[?]) et le gaspareau (*Alosa pseudoharengus*) étant les aliments dominants. Les stocks hybrides croissent plus rapidement, mais atteignent une longueur asymptotique légèrement plus petite que le touladi. Les hybrides de F_1 sont les premiers à atteindre la maturité sexuelle, 34% des mâles et 4% des femelles frayant à l'âge II. La maturité la plus hâtive est atteinte à l'âge III pour la progéniture de rétrocroisements, par contraste avec le touladi qui atteint la maturité sexuelle en général aux âges VI et VII. Les descendants de rétrocroisements ont une distribution thermique et bathymétrique légèrement plus étendue en été que celle du touladi, alors que les hybrides de F_1 ont tendance à se concentrer dans la thermocline. Les taux de mortalité annuelle totale (attribuée en grande partie à la prédation par la lamproie marine, *Petromyzon marinus*) varient des 62 à 95% pour tous les stocks implantés.

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REHABILITATION of trout populations in Lake Huron following the invasion of the sea lamprey (*Petromyzon marinus*) and subsequent decimation of the native lake trout (*Salvelinus namaycush*), (Fry 1953; Eschmeyer 1957; Lawrie 1970) has been the objective of a two-stage program coordinated by the Great Lakes Fishery Commission. The first stage is a reduction of sea lamprey populations to minimum levels of abundance, and the second is the establishment of trout stocks capable of sustaining themselves under predation by residual sea lamprey populations and exploitation by the fisheries.

The provision of a suitable replacement for the native lake trout has been the objective of a research program in selective breeding of splake hybrids (*S. fontinalis* × *S. namaycush*) initiated in 1957 by the Ontario Ministry of Natural Resources (formerly Ontario Department of Lands

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and Forests). The laboratory aspects of the program including studies of behavior, physiology, and genetics resulting in the development of selection criteria have been described by Tait (1959, 1970), Christie (1960), Ihssen (1973), Ayles and Berst (1973), Ayles (1974) and Ihssen and Tait (1974). Field studies of the suitability of various stocks have been reported by Budd (1957), Martin and Baldwin (1960), Straight (1969), Berst and Spangler (1970), Fraser (1972), and Berst and Payne (1974). The objective of this paper is to describe the habits and population dynamics of planted backcrosses (F_2 splake ♂ × lake trout ♀) in Lake Huron in relation to results obtained by planting F_1 splake and lake trout.

Results presented here span two decades of experience with various lake trout and hybrid trout stocks which were generally not coexistent in time or space. This condition precludes rigorous comparisons between stocks because the fish community of Lake Huron has undergone dramatic changes during the same period of time (Berst and Spangler 1973). Nevertheless, we have presented our findings in a comparative format with the conviction that the collective agreement of a number of minor differences is supportive of a general distinction between stocks.

Materials and Methods

This report is based mainly on 913 recoveries from a 1967 planting of 48,000 yearling backcrosses in South Bay (45°35′N; 82°00′W) of Lake Huron and 377 age II recaptures of yearling backcrosses planted in the main basin of Lake Huron by the state of Michigan in 1973.

The male parents for the South Bay planting were 3- and 4-yr-old F_2 splake that had been selected for early maturity and deep swimming ability by the method of Tait (1970). The female parents were wild lake trout taken during spawning season from Lake Manitou (Manitoulin Island). The progeny were reared at Tarentorus Trout Rearing Station, Sault Ste. Marie, Ontario. The backcrosses averaged 9.1-cm fork length and 52.9 g when planted during late June and early July, 1967, and bore left ventral and adipose clips.

During 1973, 486,000 yearling backcrosses marked with a right pectoral clip and averaging 14.5 cm long were planted in United States waters of Lake Huron by the state of Michigan (R. Eshenroder personal communication). These fish were the progeny of selected splake males and female lake trout. The male parents were the progeny of all possible combinations of crosses of F_2, F_3, and F_4 parents that had been selected for early maturity and the ability to retain swimbladder gas by the method of Tait (1970). The female parents were a mixture of wild lake trout from Lake Superior (16% of the eggs taken), Green Lake, Wisconsin (62%), and first generation hatchery lake trout (22%) from the Marquette, Michigan hatchery (R. Poynter personal communication).

Recapture data were obtained by the Lake Huron Research Unit primarily from the experimental poundnets and gillnets fished in South Bay. Additional information was obtained by sampling Canadian commercial catches from Lake Huron and South Bay. Samples from southern Lake Huron of backcrosses stocked in United States waters were obtained by the Lake Huron Fisheries Assessment Unit from Purdy Fisheries at Point Edward, Ontario.

The primary sources of data on the performance of F_1 splake and native and planted lake trout were the reports of Berst and Spangler (1970), Budd and Fry (1960), and Tomkins (1951) supplemented by unpublished data from the files of the Lake Huron Research Unit at South Bay.

Results

Diet

Stomachs from 58 lake trout backcrosses (age II–V) from South Bay indicated that the diet was mostly fish, as it was with F_1 splake of the same age-groups, consisting mainly of rainbow smelt, *Osmerus mordax* (present in 40% of the samples containing food), sticklebacks, *Pungitius*(?) (20%), and alewives, *Alosa pseudoharengus* (15%).

Fry (1948), in describing the seasonal occurrence of food organisms in the stomachs of native lake trout from South Bay, showed that invertebrate benthic organisms occurred in 14% of 165 trout stomachs containing food in the June and July samples and that fish were present in almost all stomach samples taken during the open-water season. Smelt were the dominant food organisms (40%) followed by coregonines (23%). Alewives, an important item in stomachs from backcrosses and F_1 splake during 1967–69, were not seen in South Bay until 1951 (Coble 1967).

Growth

Growth of the backcrosses in South Bay was similar to that of the F_1 hybrids planted in Burnt Island Bay (Berst and Spangler 1970) and exceeded that of planted lake trout in South Bay and native lake trout in Georgian Bay (Fig. 1). Both strains of splake attained fork lengths of 40 cm by the end of their 2nd yr in the lake, and by age IV, averaged almost 5 cm larger than planted lake trout. The 1973 Michigan planting of backcrosses averaged 37 cm after 1 yr in the lake. Von Bertalanffy growth curves for the South Bay backcrosses, F_1 splake, and planted lake trout

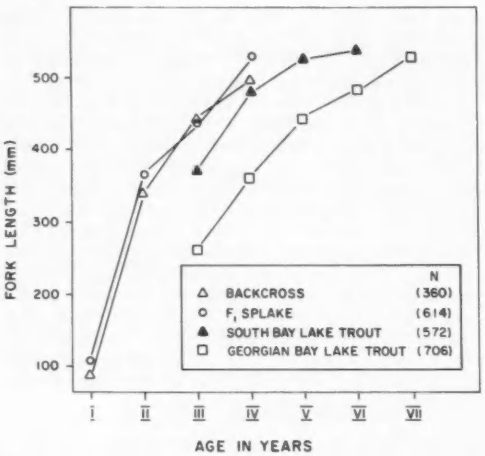

FIG. 1. Growth of planted backcrosses, F_1 splake (*Salvelinus namaycush* × *S. fontinalis*) (Berst and Spangler 1970), planted lake trout (*S. namaycush*) in South Bay (Budd and Fry 1960), and native lake trout in Georgian Bay (Tomkins 1951). Plotted points are averages for fish taken in poundnets during June, with the exception of the Georgian Bay trout, which were taken by large mesh gillnets and baited hook lines.

were fitted to tag and recapture data (Fabens 1965) to compare asymptotic lengths. The estimated growth parameters were as follows:

	Growth coefficient (k)	Asymptotic fork length (cm)
Backcrosses	−0.719	53.9
F_1 splake	−1.102	54.4
Planted lake trout	−0.311	62.0

This analysis indicates a relatively slow growth rate and greater asymptotic length for planted lake trout in contrast to a more rapid growth and somewhat smaller ultimate size for F_1 splake and backcrosses. The growth rate of the backcrosses was only slightly less than that of the F_1 splake.

LENGTH–WEIGHT

The equations for the length–weight relationships of the four stocks of fish were as follows:

Backcross	$\log W = -5.363 + 3.260 \log L$
F_1 splake	$\log W = -3.821 + 2.856 \log L$
Native lake trout	$\log W = -4.730 + 3.078 \log L$
Planted lake trout	$\log W = -5.612 + 3.245 \log L$

where W = weight in grams and L = fork length in centimeters (logarithms to the base e).

Among these stocks, the F_1 splake were heaviest for their length and the planted lake trout, lightest. For example, at a fork length of 40 cm, F_1 hybrids weighed approximately 1100 g as compared with planted lake trout of 846 g. The backcrosses and the native lake trout occupied an intermediate position between the F_1 splake and planted trout.

MATURITY

Sexual maturity was first attained in the South Bay backcrosses at age III, with 91% of the males and 5% of the females mature (Fig. 2). Only three female backcrosses were taken at age IV and two of these were mature. None of the nine male and nine female age II+ backcrosses taken by the Purdy Fisheries in the fall of 1974 were mature. F_1 splake from Burnt Island Bay attained sexual maturity at age II for 34% of the males and 4% of the females. For Georgian Bay lake trout, males and females matured predominantly at ages VI and VII, respectively (Tomkins 1951).

MIDSUMMER DEPTH AND THERMAL DISTRIBUTION

The backcrosses planted in South Bay ranged to depths of 60 m, but tended to concentrate in the 15–30-m zone with a mode at 27.5 m. The planted lake trout were more narrowly distributed throughout the 22–40-m depths with a mode at 35 m (Fig. 3 right panels). The lake trout data were based on 1958 and 1959 gillnet sets in South Bay at temperatures ranging from 4.5 to 19 C and depths from 7 to 55 m, with the ex-

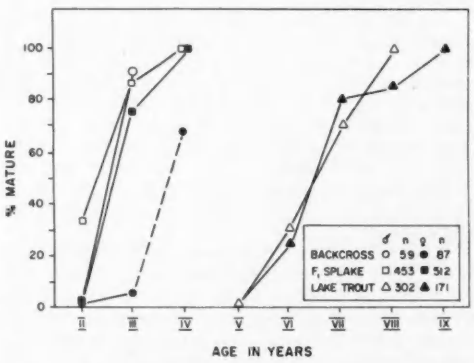

FIG. 2. Maturities of 2–4-yr-old backcrosses and F_1 splake and 5–9-yr-old lake trout. The dotted line for the female backcrosses is based on only three specimens. Sex ratios for each stock may be inferred from the inset.

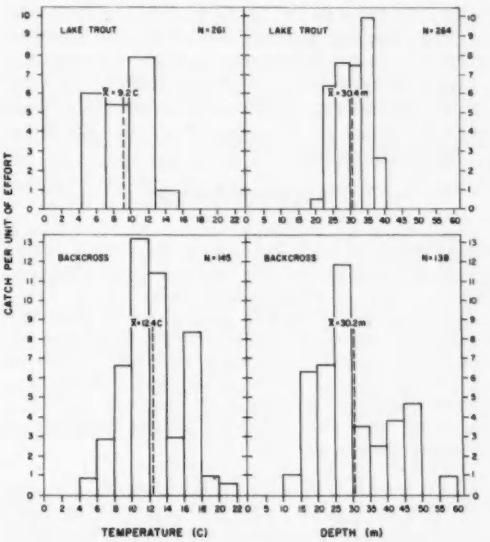

FIG. 3. Bathymetric and thermal distribution of backcrosses and lake trout from July through September in South Bay. Lake trout data were summarized by 2-fm and 5 F intervals and rescaled to metric units for plotting. Catch per unit of effort is the number of fish caught in the equivalent of one night's fishing of the experimental gillnets described by McCombie and Fry 1960 (totaling 1372 m). Means of the distributions are indicated by the broken lines.

ception that less than half a gang of effort (resulting in the capture of two lake trout) was applied at depths of 47.5–51 m. The backcross data were obtained from South Bay gillnet sets at temperatures of 5–22 C and depths of 1–60 m during 1968 and 1969.

With respect to temperature, the backcrosses were again more broadly distributed than lake trout. The mean of the thermal distribution was somewhat higher for backcrosses than for lake trout, although their modal value coincided at 11–12 C (Fig. 3 left panels). The two stocks of trout were at similar life-history stages in spite of their different ages (lake trout ages IV and V, backcross ages II and III). We feel that a rigorous comparison of these distributions is confounded more by the differing thermal regimes during the respective tenures of the lake trout and backcross plantings than by age differences.

Data on the depth and thermal distribution of F_1 splake in inland lakes of the Precambrian Shield (Martin and Baldwin 1960) and in South Bay (Budd 1957) indicate that the hybrids were concentrated in the region of the thermocline.

MORTALITY, EMIGRATION, AND LAMPREY PREDATION

The recapture of 234 backcrosses (208 in 1969, 22 in 1970, and 4 in 1971) in the June poundnet fishery in South Bay provided estimates of the total annual mortality rate for ages III–IV (89%) and IV–V (82%). Comparing these estimates with those of Budd et al. (1969) for lake trout (62% at age V, 78% at age VI, 92% at age VII) supports the contention that a major source of mortality was operative on the planted fish in South Bay from the mid-1950s to the early 1970s. The F_1 splake (ages II and III) at Burnt Island suffered extremely high mortality rates (70 and 95%, respectively, during the summers of 1967 and 1968).

These estimates of mortality rates are probably biased upward since they include emigration from the study areas, but only 18 backcrosses from the 1967 planting (1.9% of the total recaptures) were taken outside South Bay and 98% of the Burnt Island F_1 splake recoveries occurred within a radius of 32 km of the planting site. The low proportion of tag recoveries outside South Bay from planted trout (Budd et al. 1969) and the persistence of the 1944 year-class of lake trout in South Bay at a time when the species was virtually absent from the adjacent waters of Lake Huron (Fry 1953) attest to the tendency of lake trout to remain within the confines of South Bay. Thus, we judge the emigration component of the apparent mortality of these stocks to have been relatively small.

Emigration of the Michigan backcrosses from their planting sites may have occurred to a greater extent than that observed from the South Bay planting. The Michigan fish were planted at eight sites from De Tour to Port Austin (R. Eshenroder personal communication) and while recoveries in Canadian waters have been predominantly from the Point Edward area (more than 130 km from the nearest planting site) there have been scattered recaptures of these fish in the North Channel, Georgian Bay, South Bay, and along the south Manitoulin shore.

Lamprey predation on the backcrosses became apparent at age III in June of 1969 when 11% of the 208 fish examined bore healed lamprey marks. By June of 1970 this proportion had risen to 36% indicating a high degree of lamprey predation on the backcrosses during their third summer and fall in the lake (age III+). Planted lake trout in South Bay were vulnerable to lamprey attack at ages IV and V when 23 and 39%, respectively, bore lamprey marks (Budd et al. 1969). The F_1 splake at Burnt Island were vulnerable to lamprey attacks at ages II and III

as indicated by wounding rates in excess of 20% during the summers of 1967 and 1968. While lamprey predation was operative on different age-classes of the various stocks, the planted fish were always vulnerable to lamprey predation when they had attained a size of approximately 40 cm (Berst and Spangler 1970).

Discussion

Trial plantings of lake trout, F_1 splake, and lake trout backcrosses show that appreciable acceleration in growth and maturity can be achieved by planting hybrids. The rapid growth of the F_1 hybrids is clearly retained to a significant degree in the lake trout backcrosses. The maturation of backcross males, while not quite as rapid as the F_1 males, represents a gain in maturity of 2 yr compared to Georgian Bay lake trout (Tomkins 1951) and 3 yr compared to South Bay trout (Budd and Fry 1960). Similarly, the onset of maturity for backcross females preceded that of South Bay lake trout by 4 yr.

There is little evidence that the various hybrid stocks differed greatly from native and planted lake trout in their food habits or spatial distribution. The backcrosses in southern Lake Huron frequented the shallower water nearshore in the spring and fall (M. Purdy personal communication). In South Bay, the backcrosses occupied the cooler water of the thermocline and hypolimnion from July to September. The backcrosses demonstrated somewhat broader thermal and bathymetric distributions than did lake trout during the summer stratification period, while the F_1 splake tended to concentrate in the thermocline (Martin and Baldwin 1960).

Rehabilitation of a Lake Huron trout population in the presence of lamprey would require the introduction of a stock that matures in advance of significant reduction by sea lamprey predation. Also, lamprey numbers can be significantly reduced (and have been) by chemical control methods, but residual lamprey populations will continue to prey upon suitably large salmonids in the Great Lakes. We also anticipate increased exploitation pressure by commercial and recreational users on any trout stock that may be established in Lake Huron. With these considerations in mind, and because the chemical approach to lamprey control has been strongly questioned on environmental grounds (Hasler 1973, Anon. 1975), we believe that early maturity is an essential characteristic in the selection of a stock for trout rehabilitation in the Great Lakes. That this end may be achieved in part by rigorous selection, hybridization, and backcrossing is evident in the results of this and previous field studies. Further identification of desirable characteristics for planted stocks, coupled with modern techniques of genetic manipulation, will undoubtedly lead to additional gains in performance relative to the results achieved by the planting of conventional stocks.

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Viruses Associated with Lymphocystis Disease and Dermal Sarcoma of Walleye (*Stizostedion vitreum vitreum*)

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Gross examination of a spawning run of walleye (*Stizostedion vitreum vitreum*) showed a large proportion of fish to have tumors on the body and fins that appeared to be characteristic of lymphocystis disease. Light and electron microscopic examination revealed the presence of two distinct tumor types. One was characteristic of lymphocystis, consisting of typical enlarged nonneoplastic cells surrounded by hyaline layers and containing many 260 nm diameter lymphocystis virus particles in the cytoplasm. The other tumor, referred to as a dermal sarcoma, consisted of a solid mass of normal-sized cells and contained in the cytoplasm large numbers of 135 nm diameter virus particles referred to as walleye dermal sarcoma (WDS) virus. The WDS virus was similar in appearance to the leukoviruses and, with its outer layer sectioned tangentially, exhibited symmetry like a member of a leukovirus group designated by Fenner as subgenus C.

YAMAMOTO, T., R. D. MACDONALD, D. C. GILLESPIE, AND R. K. KELLY. 1976. Viruses associated with lymphocystis disease and dermal sarcoma of walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 33: 2408–2419.

L'examen macroscopique de dorés jaunes (*Stizostedion vitreum vitreum*) en voie de fraie révèle, chez une forte proportion des poissons, la présence de tumeurs tant sur le corps que sur les nageoires, et qui semblent caractéristiques de la lymphocytose. L'examen aux microscopes photonique et électronique démontre deux types distincts de tumeurs. Un type est caractéristique de la lymphocytose, constitué de cellules non-néoplastiques renflées entourées de couches hyalines et contenant dans le cytoplasme plusieurs particules de virus lymphocystiques de 260 nm de diamètre. L'autre type, désigné sous le nom de dermasarcome, consiste en une solide masse de cellules de taille normale et contient dans le cytoplasme un grand nombre de particules de virus de 135 nm de diamètre, appelés virus de la dermasarcome du doré (WDS). Le virus de la WDS ressemble aux leukovirus et, après sectionnement tangentiel de sa couche externe, montre une symétrie semblable à celle de leukovirus subgenre C (selon F. Fenner).

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LYMPHOCYSTIS disease in walleye (*Stizostedion vitreum vitreum*) has been recognized for many years (Weissenberg 1965) and the associated virus was initially described by Walker (1962). A similar disease and associated virus exists for a number of other freshwater and marine species of fishes as reported by several investigators (Templeman 1965; Walker and Weissenberg 1965; Wolf 1966; Zwillenberg and Wolf 1968; Howse and Christmas 1971; Russell 1974). The typically enlarged cells, surrounded by a hyaline layer and containing many cytoplasmic virus particles, are recognized in both freshwater and marine species.

In addition to the above type of tumor, Walker in a series of papers (1957, 1958, and 1969a) noted two other virus associated types in *Stizostedion vitreum vitreum*. The first he called a dermal sarcoma and reported that the cells were associated with 100 nm surface-budded particles. The second was an epidermal hyperplasia of walleye associated with smaller 80 nm virus particles. This report describes a situation similar, if not identical, to the former described by Walker. Two different tumors of walleye with their asso-

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TABLE 1. Incidence of tumors (lymphocystis tumors and dermal sarcomas) on walleye[a] (*Stizostedion vitreum vitreum*) taken at spawning time at Crean Lake, Prince Albert National Park in May 1975.

Size[b]	Males	Females	Both sexes
Small	7/77 (9%)	27/91 (30%)	34/168 (20%)
Medium	14/195 (7%)	26/262 (10%)	40/457 (9%)
Large	0/65 (0%)	0/10 (0%)	0/75 (0%)
Total	21/337 (6%)	53/363 (15%)	74/700 (11%)

[a]Examination and count made by J. Twanow.
[b]The fish were not weighed but the size grouping approximates 250–600 g for small, 600–1200 g for medium, and 1200–2500 g for large.

ciated viruses were found during a spring spawning run in Prince Albert National Park, Saskatchewan.

Materials and Methods

Walleye were trapped during late April to early May, 1975 during their spawning run as they passed through the lower narrows between Crean Lake and Hanging Heart Lake in Prince Albert National Park. The primary purpose of the trapping was to obtain eggs and sperm but, at the same time, fish carrying tumors were placed in a holding tank for laboratory examination. Tumors were removed and fixed for electron microscopy or frozen for future examination. The walleye, whose tumors were examined microscopically, ranged from 39 to 51 cm long and averaged 43 cm.

Tumor tissue for light microscopy was fixed in 10% buffered formaldehyde solution and sections were stained with hematoxylin and eosin (H & E), toluidine blue, or Feulgen reagents for DNA.

Specimens for electron microscopy were fixed immediately upon removal of the fish from the water either in 3% buffered gluteraldehyde, pH 7.2, or 2% buffered osmium tetroxide, pH 7.3. The tissue was embedded in Epon 812, sectioned with a diamond knife, and stained with 3% uranyl acetate and lead citrate. Electron micrographs were made on 35-mm Kodak-positive type film using a Philips 200 electron microscope at 60 kV with double condenser illumination.

Results

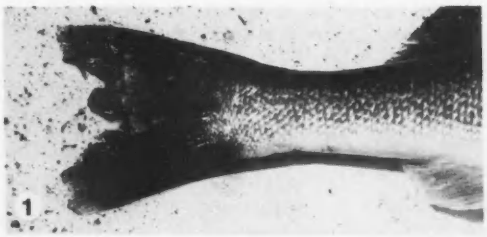
Incidence of Tumors on Walleye

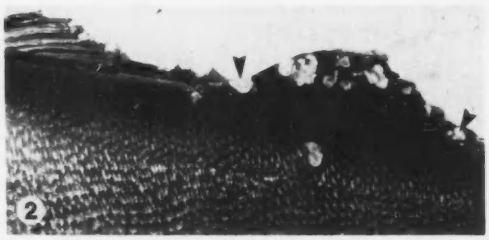
Walleye were trapped during their spawning run and examined for the presence of lymphocystis tumors on the surface of the skin. Over several days, 700 fish were randomly selected. Examination of these specimens revealed an average tumor incidence of 11%. The fish were grouped into three lots according to size, which roughly categorized them as young (including prespawners), medium and older fish. Table 1 shows the incidence of tumors according to sex and relative size. The incidence of growths on small female walleye averaged 30%, while corresponding males averaged 9%. The medium-sized fish averaged 10% for females and 7% for males. None of the large fish was found to have skin tumors. Not only did the smaller and presumably younger fish have a higher incidence of tumors, but random observations indicated that they also had larger numbers of tumors scattered over their bodies, particularly on the dorsal and caudal fins (Fig. 1).

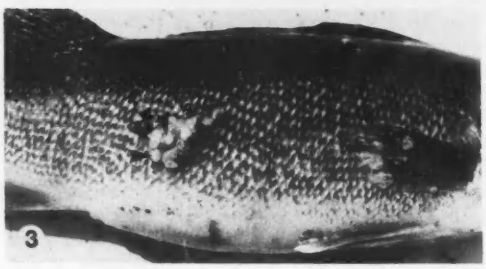
At the time of sampling in early May, it was thought that all the tumors were of the lymphocystis type and as a result accurate records of tissue materials fixed for light and electron microscopy were not maintained. When the presence of two distinct tumors became evident, frozen tumor tissues which had been taken from approximately 30 fish were reexamined at the Edmonton Laboratory to determine the tumor type. A binocular microscope, magnifying 16×, was used to differentiate the typical mulberry-like soft tissue of lymphocystis from the more solid white tumors referred to as walleye dermal sarcoma (WDS). Sizes of both tumors varied. The maximum size of both was 10 mm diam; the average size of the WDS tumor was 5 mm diam and of the lymphocystis tumor 3 mm. Counts of the two tumor types showed that there were twice as many dermal sarcomas as there were lymphocystis tumors.

In addition to the above, an independent analysis of 20 fish was made at the Freshwater Institute with the following results: 8 WDS tumors; 4 lymphocystis tumors; 4 mixed tumors, or both types present on the same fish; 2 undetermined (a very small type probably early WDS); and 2 without visible lesions. Therefore, there appeared to be agreement on the approximate ratio of 2:1 for dermal sarcomas to lymphocystis tumors.

Examination of photographs of walleye taken at the trapping site revealed that in some fish it







FIGURES 1–4

FIG. 1. Walleye (*Stizostedion vitreum vitreum*) showing typical lymphocystis tumors on the caudal fin: FIG. 2. Walleye with lymphocystis tumors on the soft dorsal fin. Some of the more round and paler tumors (arrows) may be dermal sarcomas; FIG. 3. Walleye with lymphphocystis tumors and dermal sarcomas on the body. The soft lymphocystis tumors are irregular in size and shape, while the derman sarcomas (arrows) tend to be paler and more spherical. Lymphocystis tumors can also be observed on the pectoral fin; FIG. 4. Light micrograph of lymphocystis tumor sectioned to show the epithelial cell layer covering the tumor cells, the grossly hypertrophied lymphocystis cells, and the layer of hyaline substance surrounding these cells. H & E stain, × 200.

was possible to recognize both tumor types. Figure 1 shows lymphocystis tumors on the caudal fin, while Fig. 2 shows both types of tumors present on the soft dorsal fin. Figure 3 shows lymphocystis tumors present on the pectoral fin and lymphocystis tumors and dermal sarcomas on the abdomen. The close association of the two types of tumors is noteworthy.

ASSOCIATION OF LYMPHOCYSTIS VIRUS WITH LYMPHOCYSTIS CELLS AND A SMALLER VIRUS WITH DERMAL SARCOMA CELLS

Tumor tissues from 15 different walleye were examined with the light microscope or the electron microscope, and in some instances by both. The light microscope showed many of the tumors to be composed of typical lymphocystis cells consisting of grossly enlarged cells surrounded by a thick hyaline layer (Fig. 4). These cells, when stained by the Feulgen method, showed the presence of large amounts of cytoplasmic DNA. When stained with alcian blue the hyaline layer showed the presence of mucoolysaccharides. In addition, there were patches of cells with normal appearance between the lymphocystis cells.

In other tumors the typically enlarged cells were absent and the tissue mass consisted of irregularly shaped but normal-sized cells (Fig. 5). These sarcoma cells were irregularly arranged

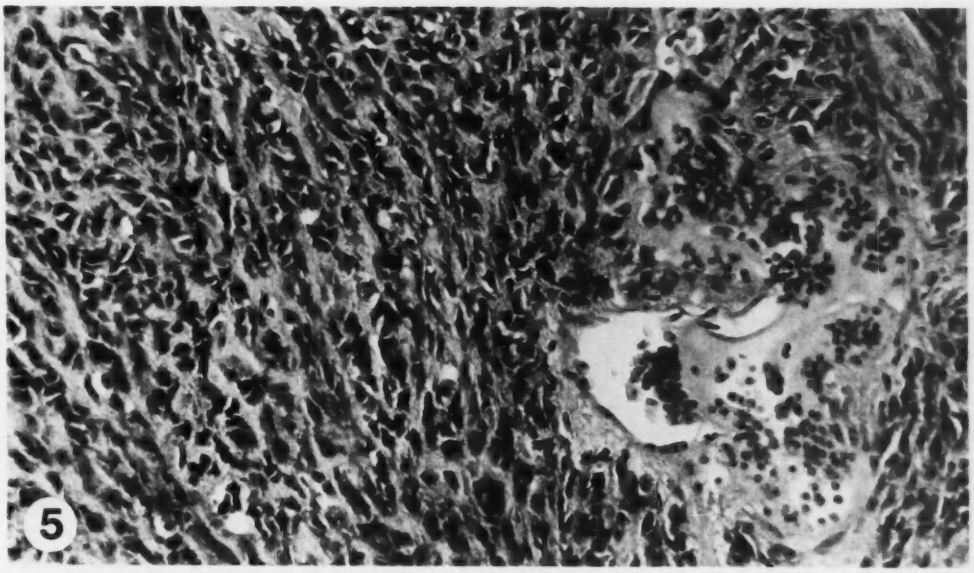


FIG. 5. Light micrograph of a section of dermal sarcoma showing disorganized arrangement of cells. The tumor mass (fish specimen 7, Table 2) is traversed by a network of capillaries containing red blood cells. H & E stain, × 600.

TABLE 2. Comparison of cell types and virus associated with tumors of walleye. +, is the presence of the indicated cell type; 0, is the absence of the indicated cell type; ±, indicates only a few lymphocystis cells present in the tumor mass. LV = lymphocystis virus.

Fish specimen no.	Tumor type observed with the light microscope		Virus observed with the electron microscope
	Lymphocystis	Dermal sarcoma	
1	±	+	WDS
2	+	0	LV
3	+	0	LV
4	0	+	LV
5	0	+	WDS
6	+	+	WDS, LV
7	±	+	WDS

and in some areas occurred in whorls. The electron microscope showed the cell surface to be highly interdigitated so that it was difficult to differentiate the cell boundaries from the endoplasmic reticulum (Fig. 6). The nucleus of the dermal sarcoma cells was stained lightly with hematoxylin and eosin (Fig. 5) and the electron microscope did not reveal any unusual nuclear features (Fig. 6).

Table 2 shows data obtained from light and electron microscope examination of tumors taken from seven fish specimens. Some were typical lymphocystis tumors consisting of lymphocystis cells and containing large numbers of lymphocystis virus particles of 260 nm diam (Fig. 7, 8, 9, and 10). Other tumors were of the dermal sarcoma type with the cells containing 135 nm diam virus particles in the cytoplasm (Fig. 6 and 11). Henceforth, this virus will be referred to as the WDS virus. Some of the dermal sarcomatous tissues were found to contain a few lymphocystis cells embedded in the cell mass (Fig. 12). These data indicated that the two virus infections may coexist in the same fish at the same time and even in the same mass of tissue. Light microscope examination of fish specimen 4 in Table 2

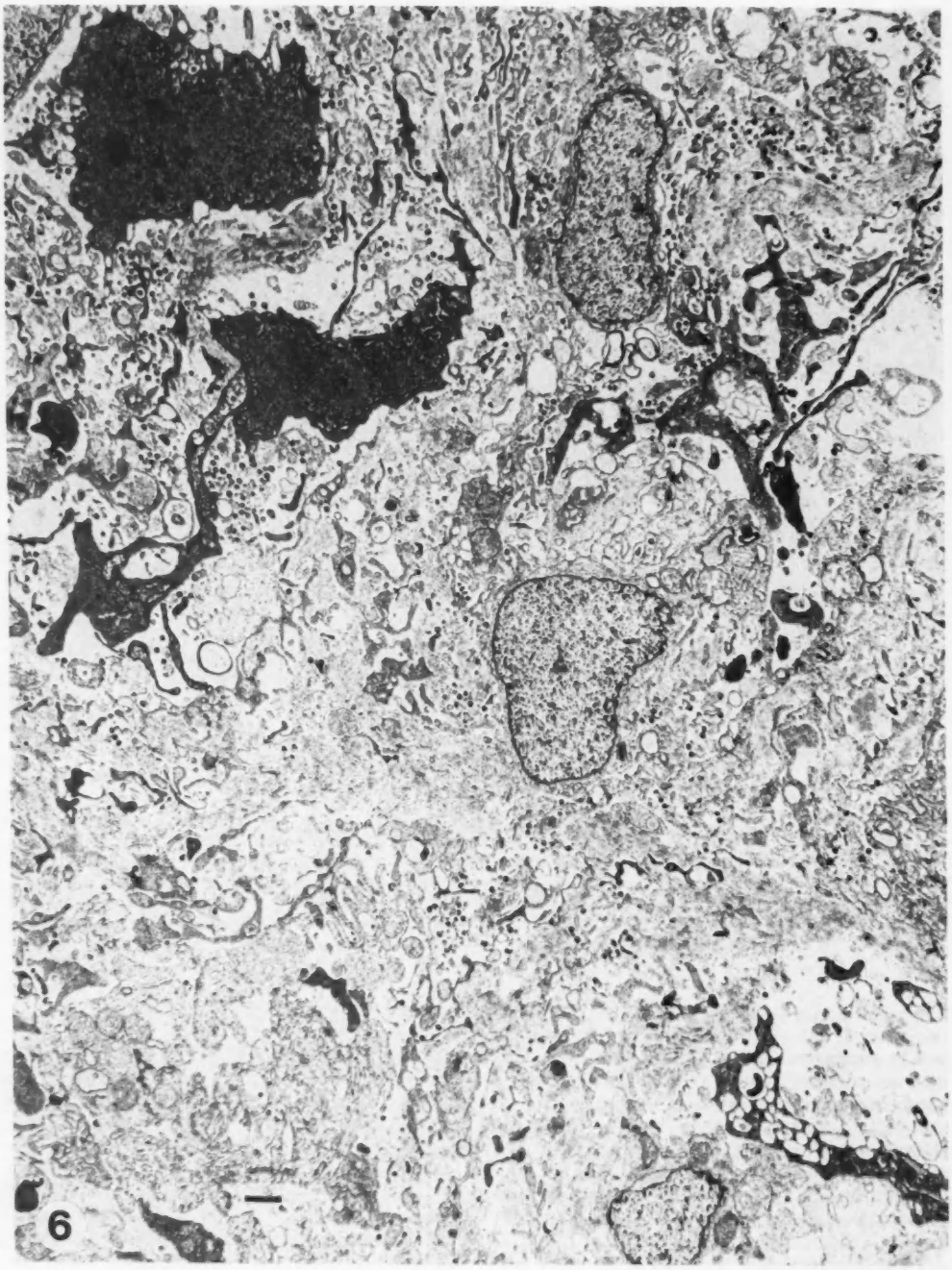


FIG. 6. Low magnification electron micrograph of thin section of dermal sarcoma showing the presence of highly interdigitated tumor cells. Virus are associated with most of the cells. Line indicates a measure of 1.0 μm.

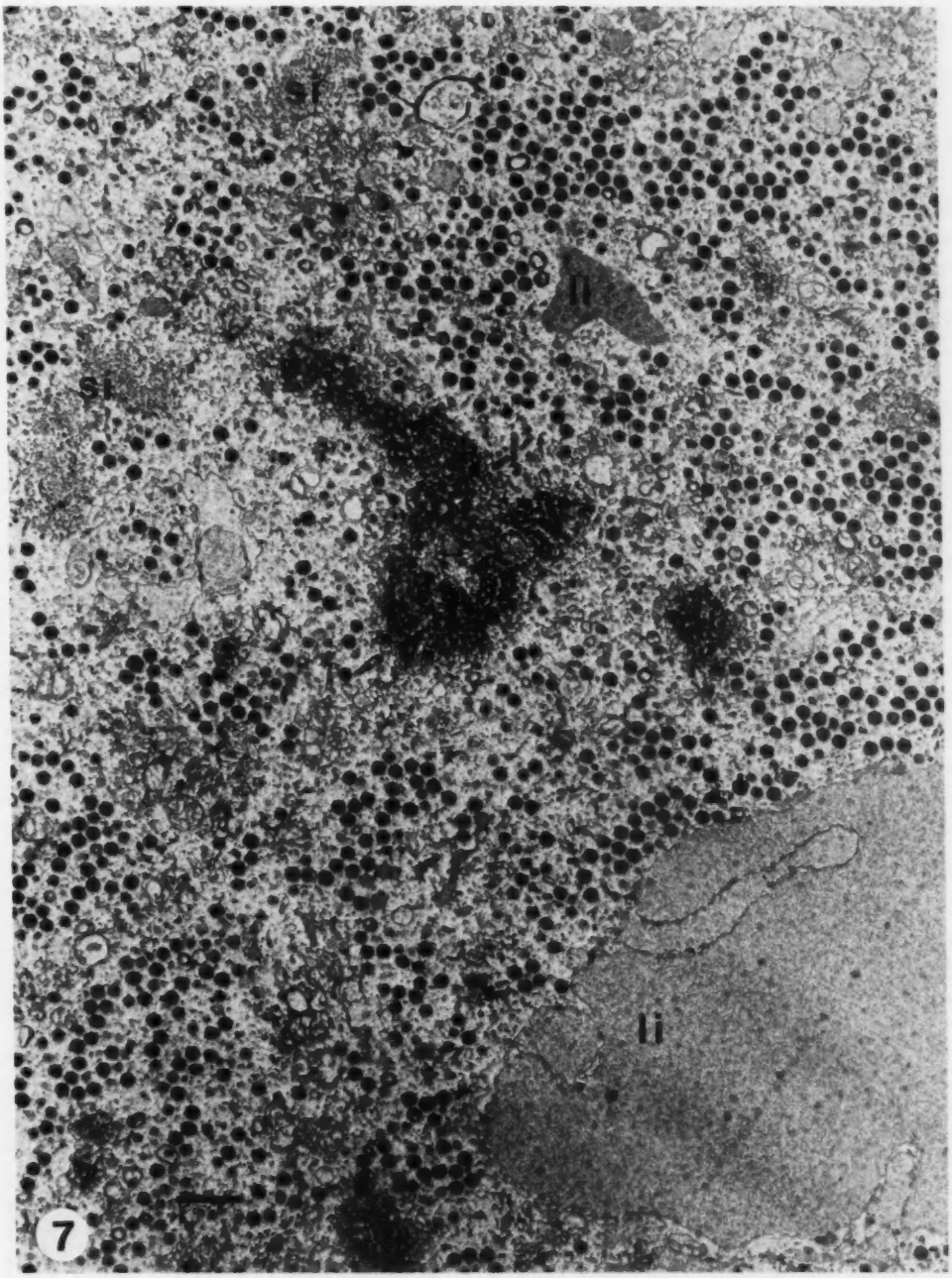
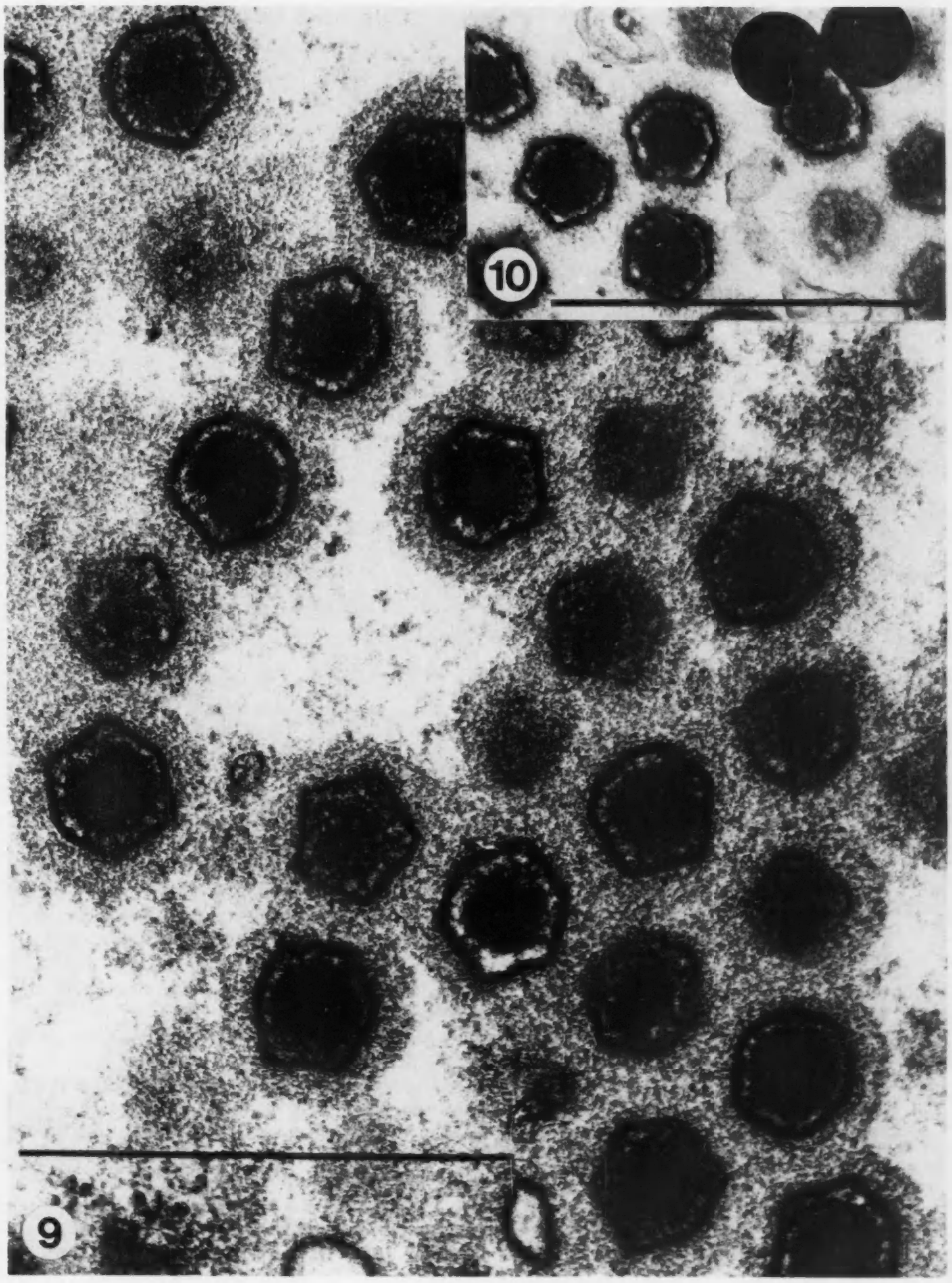


FIG. 7. Low magnification electron micrograph of thin section of large mature lymphocystis cell. The virus particles are found throughout the cytoplasm. Three different types of inclusion areas are often found in these mature cells. The light gray stippled inclusions (si) are normally associated with virus formation. The dark granular inclusion (di) and the lighter staining inclusion (li) do not appear to be directly associated with virus formation. The nucleus of the cell is not in the section area. Bar line is 10 μm.

FIG. 8. Low magnification electron micrograph of thin section of lymphocystis cell containing large numbers of lymphocystis virus. A portion of cell is shown to illustrate the nature of hyaline material surrounding the outer limits of the cell. The cell is adjacent to a capillary containing blood cells and is separated from it by a layer of connective tissue. Line indicates a measure of 1.0 μm.



FIGURES 9 AND 10

FIG. 9. Electron micrograph of thin section of lymphocystis cell showing the typical lymphocystis virus in the cytoplasm. This photograph shows well the fibrous layer surrounding the capsid. Line indicates a measure of 1.0 μm. FIG. 10. Lymphocystis virus sectioned and photographed with latex particles measuring 265 nm diam. Line indicates a measure of 1.0 μm.

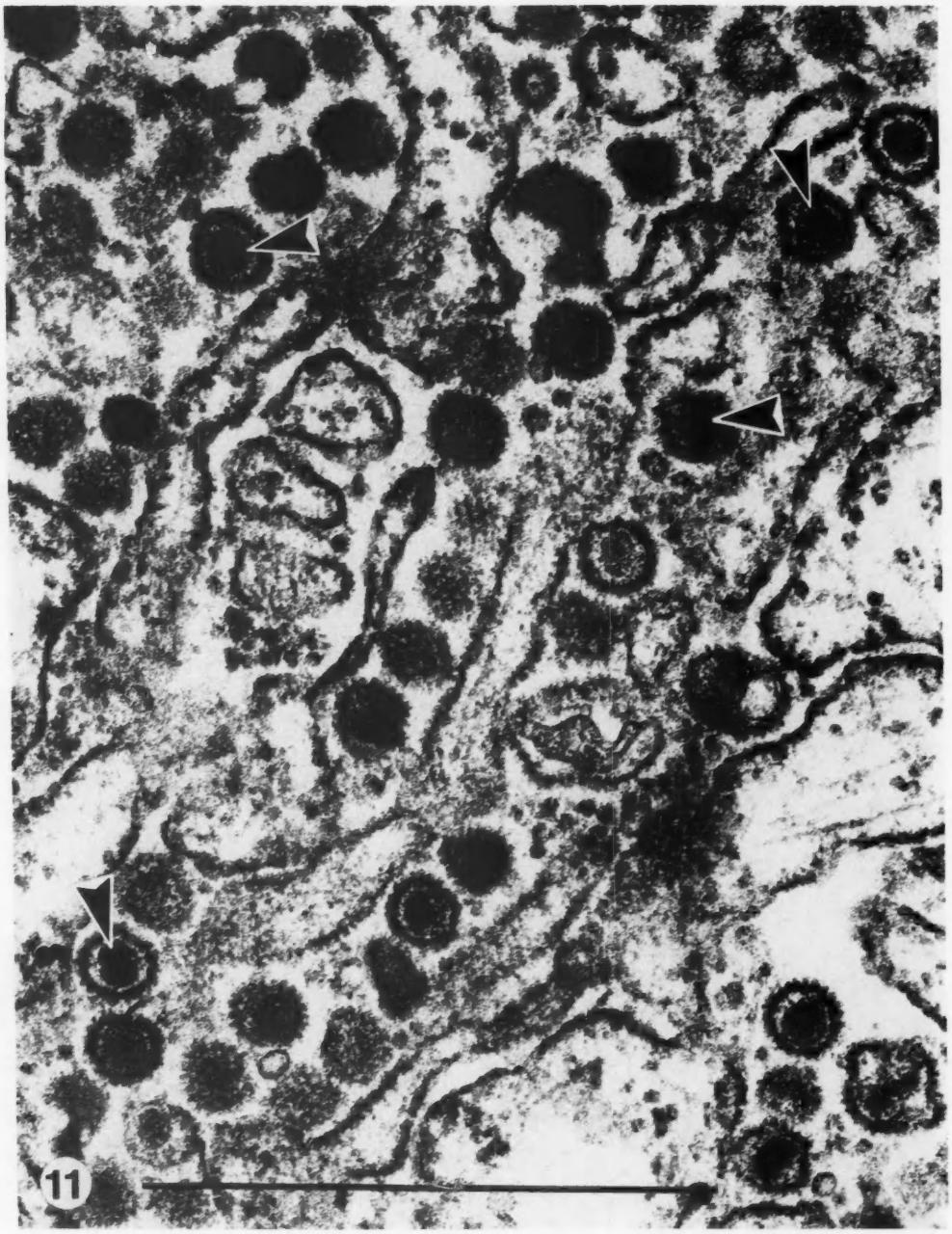


FIG. 11. Electron micrograph of thin section of walleye sarcoma cell associated with typical virus particles measuring 135 nm diam. The center of the particles varies from light to densely staining material. Some particles appear to have an inner core (arrows). The outer layer of the particles shows a regular arrangement of spicules. Particles sectioned tangentially show a regular arrangement of the spicules on the outer coat. Line indicates a measure of 1.0 μm.

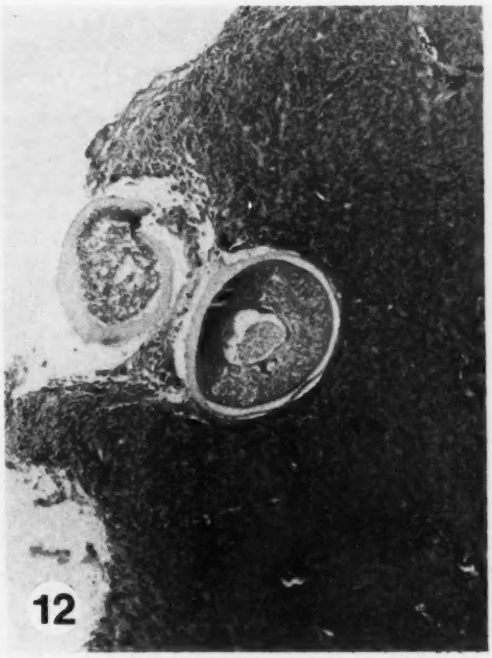


FIG. 12. Low power light micrograph of dermal sarcoma (from fish specimen No. 7, Table 2) showing two lymphocystis cells embedded in it. H & E stain, × 100.

revealed the presence of sarcomatous tissue only, while the portion of the tumor sampled for electron microscopy contained lymphocystis cells and lymphocystis virus. Tumors taken from specimen 6 showed the presence of mixed tumors which consisted of sarcoma cells and lymphocystis cells containing WDS virus and lymphocystis virus, respectively.

Careful examination of both the lymphocystis cell and the WDS cells showed that the two viruses never existed together in the same cell and are distinct viruses. Examination of connective tissue surrounding the lymphocystis cells in bona fide lymphocystis tumors did not show the presence of WDS virus. Thus, the presence of WDS virus was limited to the sarcomatous tissues. Although the lymphocystis tumor and the dermal sarcoma contained a good blood supply, none of the red cells at any time were found to be infected with either virus as determined by electron microscope examination.

MORPHOLOGICAL COMPARISON OF LYMPHOCYSTIS VIRUS AND WDS VIRUS

The lymphocystis virus of walleye had a capsid structure which had an icosahedral symmetry and measured 260 nm diam (Fig. 9 and 10). The capsid did not appear to be composed of identifiable capsomeres or morphological units and in addition was covered with an amorphous unstructured layer 20–60 nm thick, probably consisting of irregular protein filaments. This layer gave an outside dimension to the virus particle of 300–380 nm (Fig. 9).

The WDS virus, also associated with the cytoplasm, was smaller than the lymphocystis virus and measured 135 nm diam. The structural arrangement of the outermost layer became evident when the particles in thin sections were cut tangentially. The stud-like structures or spicules present on the surface appeared to have a regular arrangement. From the numbers and arrangement of these, it was estimated that the virus envelope may be composed of 162 of these structures.

The DNA nature of lymphocystis virus is well established and was readily demonstrated by the Feulgen reaction which showed large amounts of DNA in the cytoplasm of lymphocystis cells. In contrast, the negative Feulgen reaction in the cytoplasm of cells containing dermal sarcoma virus suggested that the WDS virus lacked DNA.

Examination of many thin sections of virus-containing cells revealed some particles in the process of formation from membranes (Fig. 13). Because of the highly interdigitating cell membranes it was difficult to determine whether the virus particles were released to the exterior of the cell or into vesicles within the cells. Virus particles never appeared mature within the cytoplasmic matrix. The evidence obtained in these photographs indicate that WDS virions mature at the cytoplasmic membrane and are released by pinching off, as is the case with many RNA tumor viruses.

Discussion

The lymphocystis cell obtained its name in 1904 when Woodcock considered it to be a life stage of a parasite present in plaice and flounders (reviewed by Weissenberg 1965). Since then the name has persisted even though it has been shown to be a virus-induced, enlarged cell. Undoubtedly the terms lymphocystis cell and lymphocystis virus have become well accepted and presumably will continue to be used.

The dermal sarcoma of walleye as distinct from lymphocystis has been described in the past by Walker (1947, 1958). Interestingly, he also noted the close association of the lymphocystis warts and the sarcomatous growths. He observed that the two types of tumors could be

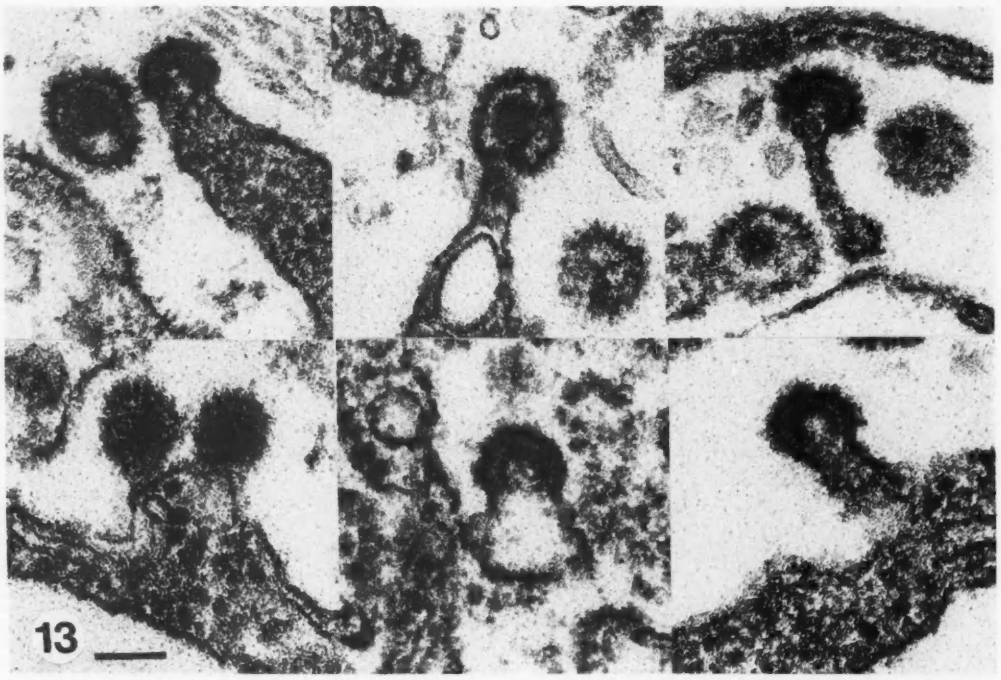


FIG. 13. Photographs showing appearance of some WDS virus particules budding off from the cell membrane. Line measures 0.1 μm.

found together in the same lump of tissue. In a more recent paper, Walker (1969a) described a dermal sarcoma associated with a virus measuring 100 nm diam. Walker's description of the sarcomatous growths in walleye coincides exactly with our observations on these growths; we have, therefore, adopted Walker's term, dermal sarcoma, to describe the condition and we refer to the associated virus as the WDS virus. This adoption of nomenclature was made even though the virus observed by us appears to be slightly larger than those reported by Walker. The similar nature of virus maturation observed by Walker and us indicates that the viruses are possibly the same or related. The epidermal hyperplasia in *Stizostedion* that Walker (1969b) also described was not evident in our samples, nor were any of the 80-nm virus particles which he found associated with this condition.

The fact that both the lymphocystis tumor and the dermal sarcoma were found on 10% of the fish population indicates that the disease is common in the walleye species. Unfortunately, little is known about the time of infection or general effect of infection on the fish population. From the higher incidence of tumors in younger fish they may, in fact, be infected very early in life. Templeman (1965) reported that certain workers found walleye without lymphocystis disease to be larger by about 5% than those with lymphocystis disease. This finding would suggest that infection may reduce the growth of the walleye by about 5%. If, however, the infection were to occur at a much earlier age, the effect on the walleye population may be much greater; but at the present time the mortality rate of the very young following infection is unknown.

The close association of lymphocystis disease and dermal sarcomas is interesting, but it is not known if the presence of one virus predisposes the fish to infection by the other. Since the two viruses are not seen together in the same cell, it is unlikely that they are different stages of the same agent. All the evidence so far would indicate that infection of a cell with lymphocystis virus results in the production of a nondividing lymphocystis cell. In contrast, infection with the WDS virus results in a proliferation of the cells into a tumor consisting of many cells containing many WDS virus particles.

Although much more study of this WDS virus is required before it can be classified with any

certainty, certain similarities with other viruses can be discussed. The WDS particles most closely resembled the viruses of the leukovirus group (See Fenner et al. 1974, for a comprehensive account of these viruses). Among the leukoviruses, they were closest in size to the progressive virus of sheep and the Visna virus (Takemoto et al.), and, in common with the leukoviruses, they possessed a regular arrangement of spikes on their outer coats and exhibited densely staining cores. The latter feature distinguished the WDS particles from another group of viruses, the arenaviruses (Rowe et al. 1970). The arenaviruses also exhibit spiked outer coats but possess, instead, granular cores (Dalton et al. 1968; Murphy et al. 1969). The foregoing features, together with a mode of maturation characteristic of certain leukoviruses in which the virus appears to be formed as it buds from the host cell membrane, strongly suggest that the WDS virus is related to the leukoviruses.

Acknowledgments

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Inbreeding in Rainbow Trout (*Salmo gairdneri*)

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KINCAID, H. L. 1976. Inbreeding in rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 33: 2420–2426.

Effects of inbreeding on rainbow trout (*Salmo gairdneri*) were evaluated by a comparison of differences between inbred and outbred half-sib families reared as contemporaries during the 1st yr of life. Attention was focused on two levels of inbreeding expressed as inbreeding coefficients: F = 0.25, one generation of brother–sister matings, and F = 0.375, two generations of brother–sister matings. Although inbreeding at the F = 0.25 level in fall-spawning populations had no effect on egg hatchability, it significantly increased the frequency of crippled fry by 37.6% and significantly decreased feed conversion efficiency (5.6%), fry survival to 147 days (14.6%), and growth rate to 147 days (6%) and 364 days (23.2%). Effects of inbreeding at F = 0.375 were more pronounced; significant differences included increased frequency of crippled fry (191.5%) and decreased feed conversion efficiency (14.9%), fry survival to 147 days (29.7%), and growth rate to 147 days (13.4%) and 364 days (33.5%). Application of the total effects of inbreeding on the number of fish remaining and the weight of fish remaining in a production lot at 1 yr of age indicated losses of 17.4 and 36.6% after one generation (F = 0.25) and 47.9 and 65.4% after two generations (F = 0.375) of brother–sister mating. Similar studies on a spring-spawning population produced similar results. General breeding methods that minimize the rate of inbreeding accumulation are discussed.

KINCAID, H. L. 1976. Inbreeding in rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 33: 2420–2426.

Nous avons mesuré les effets de la consanguinité sur la truite arc-en-ciel (*Salmo gairdneri*) en comparant les différences entre des familles n'ayant qu'un parent en commun, issues de croisements consanguins et non consanguins, et élevées ensemble durant la 1re a. de vie. Notre attention a porté sur deux paliers de consanguinité exprimés comme coefficients de consanguinité: F = 0.25, une génération de croisements entre frères et sœurs, et F = 0.375, deux générations de croisements entre frères et sœurs. Bien que la consanguinité au palier F = 0.25 chez les populations frayant en automne n'affecte pas le pourcentage d'éclosion des œufs, elle augmente de façon significative la fréquence des alevins difformes (37.6%) et diminue de façon significative l'efficacité de conversion de la nourriture (5.6%), la survie des alevins à 147 jours (14.6%) et le rythme de croissance à 147 jours (6%) et à 364 jours (23.2%). Les effets de la consanguinité au palier F = 0.375 sont plus prononcés; parmi les différences significatives observées on compte une augmentation de la fréquence d'alevins difformes (191.5%); et une diminution de l'efficacité de conversion (14.9%), de survie des alevins à 147 jours (29.7%), et du rythme de croissance à 147 jours (13.4%) et à 364 jours (33.5%). Lorsqu'on applique les effets totaux de la consanguinité au nombre et au poids des poissons qui restent dans un lot de production à 1 a. d'âge, on constate une perte de 17.4 et de 36.6% après une génération (F = 0.25) et de 47.9 et de 65.4% après deux générations (F = 0.375) de croisements entre frères et sœurs. Des études semblables effectuées sur une population frayant au printemps donnent des résultats semblables. Nous discutons des méthodes générales d'élevage permettant de réduire au minimum le taux d'accumulation de la consanguinité.

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DELETERIOUS effects of inbreeding have been described mathematically by Wright (1922), Fisher (1949), Robertson (1954), and Falconer (1960) (among others), who used laboratory animals to test the model derived. Many plant and animal breeders have found the effects of inbreeding to be generally unfavorable. In contrast to the extensive literature available on domesticated animals, little definitive information has been published on the effects of inbreeding in fish species. Moav and Wohlfarth (1963) observed a 15% reduction in relative growth rate in inbred carp (*Cyprinus carpio*) produced from full-sib parents as well as an increased proportion of fish with dorsal fin anomalies. Aulstad and

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Kittelsen (1971) reported deformities in fry of rainbow trout (*Salmo gairdneri*) associated with 25% inbreeding. Ryman (1970) found lower recapture frequencies of Atlantic salmon (*S. salar*) from inbred families, suggesting lower survival in those families. Bridges (1973) estimated depressions, per 10% inbreeding, of 5.1% in fish weight and 0.4% in Formalin tolerance, at 150 days of age, in rainbow trout. Cooper (1961) reported an inbreeding depression in weight of brook trout (*Salvelinus fontinalis*) of 27.7% at 7 mo and 34.3% at 19 mo.

The purpose of this report is to present the results of studies designed to measure the effects of inbreeding in rainbow trout (*Salmo gairdneri*).

Materials and Methods

The mating system used for measuring inbreeding depression involved the mating of a single female simultaneously with both a full brother to produce an inbred full-sib family and with an unrelated male to form a related outbred family. Inbreeding depression was then estimated as the difference between these female inbred–outbred half-sib families in which the female parent was common to both families. Similar estimates were obtained from matings of a single male simultaneously with both a full sister and an unrelated female referred to as male inbred–outbred half-sib families (Kincaid 1976). All "unrelated" fish used in the matings were taken from a standard population maintained by random mating for a number of years. The resulting inbred–outbred family pairs were then reared concurrently under standardized rearing conditions from swim-up stage to 364 days of age to demonstrate the cumulative effects of inbreeding on the fish as they increased in size and age. Fish age was measured from the day of spawning. Traits on which inbreeding depression were measured include:

Eyed eggs — Percent of eggs surviving from spawning to the eyed stage at 21 days.

Eggs hatching — Percent of eggs spawned that produced living fry.

Crippled fry — Percent of fry at swim-up stage (42 days) that were abnormal (yolk-sac deformities, head deformities, back deformities, etc.). These fish were removed from the family at this time.

Mean weight — Average fish weight of a family at 84, 126, 147, 168, 189, 245, 301, and 364 days.

84 day survival — Percent of fish in the family at swim-up that survived to 84 days of age.

147 day survival — Percent of fish in the family at 84 days that survived to 147 days of age.

147 day feed conversion — Feed presented to the fish per unit gain in weight during the period from 84 to 147 days of age.

Cube root of daily gain — Calculated as cube root of mean fish weight at the end of the period minus the cube root of mean fish weight at the beginning of the period divided by the number of days in the period. This transformation of weight data was used to convert growth to a linear function of time.

Formalin LC50 — Formalin concentration in parts per million required to kill 50% of the test fish in 6-h continuous flow test at 147 days of age. Standard toxicity testing procedures were followed using 20 fish per test concentration. LC50 values were calculated by the method of Litchfield and Wilcoxon (1949).

Rearing conditions under which the studies were conducted include: water temperature, 11 ± 1 C; pH, 7.6–7.8; hardness, 426 ppm hardness as $CaCO_3$, 634 ppm total hardness; incubation, Heath overflow type; rearing units, 17.1-liter circular polyethylene tub with 2.3-liters/min gravity inflow from swim-up stage to 147 days and 1.2-m diam circular fiberglass tanks with 3.8-liter/min jetted inflows from 147 to 364 days. Loading density was held at or below 1 kg in the 17.1-liter units and 12 kg in the 1.2-m diam units.

Inbreeding depression was measured as the difference in a characteristic found between families of an inbred and outbred pair. Percent depression was inbreeding depression divided by the outbred family average.

The term "coefficient of inbreeding" (F), as used throughout this report, defines the level of inbreeding present in each of the inbred lines studied. Inbreeding level was measured from the time the parent strains were introduced to this laboratory.

During the period from the fall of 1968 to the spring of 1973, a number of inbred–outbred half-sib families at the $F = 0.25$ (one generation of brother–sister mating) level were produced each year from both the fall- and spring-spawning strains. Resulting families were then reared to 147 days to measure the effect of inbreeding up to the fingerling stage. In the 1973–74 spawning year, when 14 (5 fall- and 9 spring-spawning) $F = 0.25$ inbred lines reached sexual maturity, inbred–outbred half-sib families at the $F = 0.25$ and 0.375 levels were produced. These families were reared to 364 days to measure the total effect of inbreeding in fish to an age and size approximating the production of hatchery-reared catchable plants. The inbred lines from which brood fish for these studies were taken have been retained in our breeding program based only upon relationship to five different fish strains that have been introduced into the laboratory since 1964. Artificial selection was not applied to any of the inbred lines for hatchery production traits.

Results

Inbreeding depression data from the 1968 to 1973 period were first evaluated on a spawning year basis. Both the spring- and fall-spawning strains experienced significant inbreeding depression though a somewhat different pattern was seen in the two groups. Year to year differences in depression estimates were small; therefore, the data were pooled for the 6-yr period with equal weight given to each year class (Table 1).

TABLE 1. Inbreeding depression estimates (F = 0.25) from fall- and spring-spawning strains of rainbow trout (*Salmo gairdneri*) 1968–73. (Data are based on 49 female and 33 male inbred–outbred pairs in the fall strain and 101 and 65 pairs, respectively, in the spring strain.) *Significant ($P < 0.05$) using Student's *t*-test.

Characteristic	Common female parent		Common male parent		Avg % depression
	Outbred mean	% depression	Outbred mean	% depression	
Fall strain					
% egg hatch	61.8	−1.0	54.0	−5.3	−3.2
Mean wt (*g*), 105 days	1.2	6.0*	1.2	7.3*	6.6*
Mean wt (*g*), 147 days	3.8	7.9*	3.7	11.7*	9.8*
% survival, hatch to 147 days	74.5	6.7*	72.1	12.5*	9.6*
Formalin LC50	439.0	5.5*	402.0	6.0*	5.7*
Spring strain					
% egg hatch	57.9	−2.1	61.8	1.2	−0.4
Mean wt (*g*), 105 days	1.1	14.6*	1.1	15.5*	15.1*
Mean wt (*g*), 147 days	2.4	13.7*	2.2	9.9*	11.8*
% survival, hatch to 147 days	71.1	13.3*	67.7	32.1*	22.7*
Formalin LC50	428.0	9.4*	358.0	−4.4	2.5

TABLE 2. Calculated effect of inbreeding (F = 0.25) on production of fall- and spring-spawning strains of rainbow trout from a sample of 1000 eggs (means and depression estimates are from Table 1).

Characteristic	Fall strain		Spring strain	
	Outbred	Inbred	Outbred	Inbred
No. of eggs	1000	1000	1000	1000
% survival to 147 days	73.3	66.3	69.4	53.6
No. of fingerlings	733	663	694	536
Mean wt (*g*), 147 days	3.8	3.4	2.3	2.0
Total wt (*g*), 147 days	2785	2254	1596	1072

Inbreeding at the F = 0.25 level did not significantly affect egg hatchability in either fall- or spring-spawning populations (Table 1). However, mean weights at 105 and 147 days, percent survival, and Formalin tolerance were significantly ($P < 0.05$) depressed in both strains. When these inbreeding depression estimates are applied to samples of 1000 eggs, the effect of inbreeding at the F = 0.25 level on fish production in a hatchery is clearly demonstrated (Table 2). The net loss to the production hatchery from inbreeding at a level of F = 0.25 at 147 days would have been:

Characteristic	Fall F = 0.25 (%)	Spring F = 0.25 (%)
Loss in no. of fish	9.5	22.8
Loss in wt of fish	19.1	32.8

Inbreeding depression estimates based on the progeny of F = 0.25 inbreds of the fall-spawning strain in 1974 held for 364 days yielded further insight into the damaging effects of inbreeding to hatchery production (Table 3). Percentage hatch, fry survival, and fish weights to 147 days were similar to the earlier experimental fish (Table 1), although the depression in weights was somewhat smaller. Percentage of crippled fry was 37.6% higher than in the progeny of the outbred fish. This loss to production was not reflected in the more extensive experiments discussed earlier because crippled fry were not recorded but were discarded at swim-up when the number of fish to be carried was reduced. The source of loss to production was therefore not included in those studies. The increasing rate of depression in weight with increasing age is clearly shown by the continuous increase in percent depression from 6.1% at 147 days to 23.2% at 364 days (Table 3). This growth depression caused the weight difference between the two groups to increase continuously as age advanced. Depression in feed conversion demonstrates that the inbred fish also required an average of 5.6% more feed to pro-

TABLE 3. Inbreeding depression estimates for growth in weight and survival of the progeny from eight pairs of inbred (F = 0.25) rainbow trout of the fall-spawning strain, 1974. *Significant ($P < 0.05$) using Student's *t*-test.

Characteristic	Common female parent (*4 pairs*)		Common male parent (*4 pairs*)		
	Outbred mean	% depression	Outbred mean	% depression	Avg % depression
Eggs eyed (%)	66.5	−16.7	46.9	−65.7	−41.2
Eggs hatched (%)	64.1	−17.4	41.4	−81.8	−49.6
Fry crippled (%)	3.6	111.9*	12.0	−36.7	37.6*
Mean wt (*g*) after					
84 days	0.5	−8.3	0.6	4.6	−1.9
105 days	1.2	−8.2	1.4	7.4*	−0.4
126 days	2.4	1.0	2.7	8.8*	4.9
147 days	4.4	2.8	4.6	9.3*	6.1*
168 days	8.1	9.7*	8.6	15.5*	12.6*
189 days	14.2	13.1*	15.0	16.8*	15.0*
245 days	41.3	17.7*	39.8	14.1*	15.9*
301 days	101.0	21.7*	100.3	20.0*	20.9*
364 days	202.8	25.7*	191.3	20.8*	23.2*
Survival (%)					
Swim-up to 84 days	73.9	5.0	93.7	18.6*	11.8*
84–147 days	71.0	9.0*	89.7	20.2*	14.6*
Feed conversion (147 days)	1.3	10.4*	1.5	0.8	5.6*
Cube root of daily gain					
84–147 days	0.013	4.3	0.013	3.9	4.1
147–364 days	0.018	7.5*	0.019	9.1*	8.3*

duce the same amount of flesh. Inbreeding depression in "cube root of daily gain" for the two periods before and after 147 days again shows the difference between inbreds and outbreds in the rate at which weight was gained: this differential continued to increase throughout the 364-day testing period.

Inbreeding depression estimates from F = 0.375 inbreds of the fall populations showed a pattern similar to that of the F = 0.25 group (Table 4). Depression in "percent eggs eyed" and "percent eggs hatched" was nonsignificant and extremely variable. Percentage of crippled fry was 191% higher than in outbred half-sibs. Depression in weight increased from 16.5% at 84 days to 33.5% at 364 days. Fry survival, feed conversion, and cube root of daily gain also were significantly depressed. Depression estimates for F = 0.375 fish ranged from 0.6 to 884% higher than corresponding estimates in the F = 0.25 group.

Depression estimates from F = 0.375 inbred fish from spring populations were similar to those from the fall F = 0.375 group, although they tended to be somewhat smaller (Table 5). An unusual growth depression pattern was observed in this group from 126 to 189 days of age. The observed percent depression from 126 to 168 days decreased until no depression was present. After 168 days, however, the weight difference again appeared and increased until 364 days when it was of the same magnitude as that seen in the fall families. The reason for this apparent period of compensatory growth in the inbreds is not clear considering the rearing conditions and handling procedures were standardized in the spring and fall groups. The performance of all the inbred families in this group showed this pattern of decreasing then increasing inbreeding depression, though it was less pronounced in the male half-sib families. The end result, however, was that 147-day summaries showed inbreeding depression in the F = 0.375 lines to be somewhat lower than in F = 0.25 lines during the 1968–73 period. By 364 days, inbreeding depression was in line with that expected from the fall F = 0.375 lines.

Using the inbreeding depression estimates obtained from the 1974 studies (Tables 3, 4, and 5) the cumulative effect of inbreeding at each inbreeding level was calculated through 364 days (Table 6). The calculated percentage loss in hatchery production due to inbreeding in these three groups was:

TABLE 4. Inbreeding depression estimates for growth in weight and survival of the progeny from 21 pairs of inbred (F = 0.375) rainbow trout of the fall-spawning strain, 1974. *Significant ($P < 0.05$) using Student's *t*-test.

Characteristic	Common female parent (*11 pairs*)		Common male parent (*10 pairs*)		
	Outbred mean	% depression	Outbred mean	% depression	Avg % depression
Eggs eyed (%)	49.8	−18.4	58.5	−0.8	−9.6
Eggs hatched (%)	44.3	−0.7	41.5	−15.2	−7.9
Fry crippled (%)	11.8	163.8*	10.2	219.1*	191.5*
Mean wt (*g*) after					
84 days	0.5	4.7	0.6	28.3*	16.5*
105 days	1.3	6.3*	1.7	33.0*	19.6*
126 days	2.4	−0.6	3.1	24.5*	12.0*
147 days	4.3	2.2	5.3	24.6*	13.4*
168 days	7.9	9.5*	9.2	34.2*	21.8*
189 days	14.0	15.7*	15.7	24.5*	20.1*
245 days	40.4	30.0*	41.1	30.2*	30.1*
301 days	96.0	38.8*	91.0	29.7*	34.2*
364 days	196.3	35.6*	172.5	31.5*	33.5*
Survival (%)					
Swim-up to 84 days	49.7	29.3*	65.4	39.3*	34.3*
84–147 days	59.1	19.3*	62.3	40.1*	29.7*
Feed conversion (147 days)	1.4	12.8*	1.3	17.0*	14.9*
Cube root of daily gain					
84–147 days	0.013	1.5	0.014	7.3*	4.4*
147–364 days	0.018	17.4*	0.018	13.6*	15.5*

TABLE 5. Inbreeding depression estimates for growth in weight and survival of the progeny from 31 pairs of inbred (F = 0.375) rainbow trout of the spring-spawning strain, 1974. *Significant ($P < 0.05$) using Student's *t*-test.

Characteristic	Common female parent (*17 pairs*)		Common male parent (*14 pairs*)		
	Outbred mean	% depression	Outbred mean	% depression	Avg % depression
Eggs eyed (%)	65.6	2.9	62.7	−2.9	0.0
Eggs hatched (%)	58.7	7.2	52.5	−10.3	−1.6
Fry crippled (%)	18.6	−8.7	13.0	43.6*	17.4*
Mean wt (*g*) after					
84 days	0.5	10.2*	0.5	12.2*	11.2*
105 days	1.1	14.1*	1.1	13.5*	13.8*
126 days	2.0	10.0*	1.9	8.7*	9.3*
147 days	3.1	1.7	3.0	5.5*	3.6
168 days	5.1	−2.4	5.4	2.3	−0.1
189 days	8.9	6.2*	9.5	13.6*	9.9*
245 days	28.5	19.1*	32.3	30.2*	24.6*
301 days	61.0	24.2*	74.0	31.0*	27.6*
364 days	112.4	26.9*	132.4	31.7*	29.3*
Survival (%)					
Swim-up to 84 days	91.8	9.8*	88.5	7.4	8.6*
84–147 days	90.6	9.7*	83.7	−3.2	3.2
Feed conversion (147 days)	2.2	3.5	2.2	3.3	3.4
Cube root of daily gain					
84–147 days	0.010	0.0	0.010	1.6	0.8
147–364 days	0.016	21.0*	0.013	22.2*	21.6*

TABLE 6. Calculated effect of inbreeding on production of fall- and spring-spawning rainbow trout at two levels of inbreeding from a sample of 1,000 eggs (means and inbreeding depression estimates are from Tables 3, 4, and 5).

Characteristic	Fall strain (F = 0.25)		Fall strain (F = 0.375)		Spring strain (F = 0.375)	
	Outbred	Inbred	Outbred	Inbred	Outbred	Inbred
No. of eggs	1,000	1,000	1,000	1,000	1,000	1,000
% cripples	7.8	10.7	11.0	21.0	15.8	18.6
No. of fry	922	893	890	790	842	814
% survival to 147 days	80.5	68.7	60.7	39.7	87.2	77.1
No. of fingerlings	742	613	601	313	734	628
Mean wt (*g*), 147 days	4.5	4.2	4.8	4.2	3.1	2.9
Total wt (*g*), 147 days	3,340	2,595	2,884	1,302	2,239	1,820
Mean wt (*g*), 364 days	197.1	151.3	184.4	122.6	122.4	86.6
Total wt (*g*), 364 days	146,248	92,741	110,824	38,371	89,842	54,350

Characteristic	Fall F = 0.25 (%)	Fall F = 0.375 (%)	Spring F = 0.375 (%)
Loss in no. of fish at 147 days	17.4	47.9	14.4
Loss in wt of fish at 147 days (fingerlings)	22.3	54.9	18.7
Loss in wt of fish at 364 days (catchables)	36.6	65.4	39.5

Summary and Conclusions

Studies of fall- and spring-spawning populations of rainbow trout demonstrated that inbreeding at a level of F = 0.25, equivalent to one generation of full-sib mating, produced significant reduction in growth rate, survival, and feed conversion efficiency and increased frequencies of crippled fry. The total loss in production in number of fish and growth rate, resulting from this level of inbreeding in hatchery situations was large. In addition, the efficiency of feed conversion in inbred fish was 5.6% less than that in outbred groups. These increased fish losses, reduced growth rates, and increased feed costs greatly decrease the efficiency and increase the costs of hatchery operations.

The F = 0.375 level of inbreeding, equal to two generations of full-sib mating, yielded even higher inbreeding depression estimates than the F = 0.25 group in the fall-spawning population but somewhat lower estimates in the spring-spawning populations. The loss to total production of fish and weight of fish at 1 yr in this group was substantially higher than in the F = 0.25 group. Efficiency of feed conversion at this inbreeding level was reduced 3.4 to 14.9%. In fall-spawning fish, individual trait depression estimates measured in the F = 0.375 groups increased from 0 to 884% over those found in the F = 0.25 groups.

The inbreeding depression estimates measured in these studies are generally expected to approximate those that will be obtained in other rainbow trout populations, but wide variations may be found. Factors that will moderate or exaggerate inbreeding depression estimates in specific populations are: previous history of inbreeding, rate of inbreeding accumulation, and selection. Each of these factors will play an important role in determining the amount of genetic variation present in a specific population for inbreeding to act upon. Another factor that can effect the magnitude of depression estimates is the degree of stress applied to a population by the rearing environment. Generally higher stress situations would be expected to increase the depression experienced (Falconer 1960).

While inbreeding can be a useful tool for animal breeders, in some cases, the potential harmful effects of inbreeding in most production situations cannot be overemphasized. The primary trends exposed by the present studies show that inbreeding at the F = 0.25 level results in significant depression in fish survival, growth rate, and feed efficiency and that the magnitude of the depression increases with increasing levels of inbreeding. In addition, the reduced growth rate and feed efficiency, which is apparent by the fingerling stage, is maintained at least through the 1st yr and probably through the entire life cycle.

Personnel responsible for maintaining brood stocks must become more aware of the serious problems resulting from inbreeding so that they can adopt breeding approaches that will minimize potential future breeding problems. Current approaches to the avoidance of inbreeding fall into

four categories: 1) use of large random-mating populations, 2) rotational line crossing, 3) periodic introductions of unrelated stocks, and 4) use of hybrid populations. A source of confusion frequently experienced by brood stock managers using large random-mating populations to avoid inbreeding is that the breeding population is defined as the number of fish used to produce the next generation, not the total number of fish in the population. The rate of inbreeding accumulation in a random-mating population is also seriously affected by the number of fish of each sex actually used to produce the next generation. Examples of inbreeding rates expected with various numbers of parent fish are:

No. of fish		Inbreeding per generation
females	males	(%)
100	100	0.2
50	50	0.5
50	25	0.7
10	10	2.0
10	5	3.0
5	5	5.0
5	2	8.0

In choosing from these four approaches it should be kept in mind that although large-random mating populations and rotational line crossing reduce the rate of inbreeding accumulation, these measures do not prevent further inbreeding. All breeding systems applied to a closed population will undergo some inbreeding over a long period of time. If the population is large, however, inbreeding will occur slowly and the normal effects of selection and mutation will prevent a serious inbreeding build-up. On the other hand, the use of hybrid populations and introductions of new stocks break up the genetic combinations that cause inbreeding depression, but do not prevent the reoccurrence of inbreeding in later generations. For this reason, after a new stock is introduced and hybridized on to the old stock, consideration should be given to employing a breeding scheme to minimize future inbreeding accumulation. A second problem area with introductions is that the new stock should be carefully chosen to complement the present stock and to avoid the introduction of undesirable characteristics. The specific approach that should be adopted will differ from brood stock to brood stock depending on the existing level of inbreeding and the planned use of the brood stock in future fish production programs.

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Analysis of Seasonal Distribution Patterns of Young Largemouth Bass (*Micropterus salmoides*) by Use of Frequency-of-Capture Data[1]

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VAN DEN AVYLE, M. J. 1976. Analysis of seasonal distribution patterns of young largemouth bass (*Micropterus salmoides*) by use of frequency-of-capture data. J. Fish. Res. Board Can. 33: 2427–2432.

Frequency-of-capture data indicated that behavioral patterns of tagged age II largemouth bass (*Micropterus salmoides*) influenced catchability with shoreline electrofishing so that mid-summer population estimates were too low. The population separated into offshore and shoreline groups during the summer, and there is evidence of persistence in habitat preference from one year to the next.

Tests of catchability were based on the agreement between observed frequencies of capture and those predicted from a bivariate model that allowed mortality and migration during the study. Though frequency-of-capture data have been widely utilized in studies of terrestrial animal populations, this information has been generally ignored by fishery biologists.

VAN DEN AVYLE, M. J. 1976. Analysis of seasonal distribution patterns of young largemouth bass (*Micropterus salmoides*) by use of frequency-of-capture data. J. Fish. Res. Board Can. 33: 2427–2432.

Les données sur la fréquence des captures indiquent que le comportement d'achigans à grande bouche (*Micropterus salmoides*) d'âge II et marqués affecte leur chances de capture par pêche à l'électricité le long du rivage, de telle façon que les estimations de populations à la mi-été sont trop faibles. En été, la population se divise en un groupe hauturier et un groupe côtier, et cette préférence dans l'habitat semble persister d'une année à l'autre.

Les tests de possibilité de capture sont fondés sur l'accord entre les fréquences de capture observées et celle prédites à partir d'un modèle à deux variables tenant compte de la mortalité et de la migration au cours de l'étude. Bien que les données sur la fréquence de capture aient été largement utilisées dans les études de populations d'animaux terrestres, les biologistes des pêches ont, en général, fait peu de cas de ce genre d'information.

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DURING a study of production rates of age I and II largemouth bass (*Micropterus salmoides*), semimonthly mark and recapture population estimates showed an unusually high mortality rate of 90% from April to November 1972 (Van Den Avyle 1973). There were no independent data to support or refute the accuracy of these estimates, but Lewis and Flickinger (1967), Parker and Hasler (1959), and others have suggested that nonrandom movement of fish away from the shoreline and territoriality of young largemouth bass during the summer could affect their catchability and subsequently cause underestimation of the population size, producing erroneously high mortality rates derived by comparing spring and summer population levels.

This paper uses frequency-of-capture data to analyze whether the behavioral traits just mentioned influenced the catchability and population estimates of age II largemouth bass in a 3-ha Iowa lake. Because fish behavior, physical catchability, sampling technique, and their interactions influence the capture rate of all individuals, tests of catchability may provide behavioral information as well as evaluations of other assumptions in estimation techniques. This approach, though previously employed in studies of mammal and insect populations, has been largely unused in fishery biology.

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Materials and Methods

McFarland Lake, Story County, Iowa (S 1/2 sec. 7, T84N, R23W). is a narrow 3-ha impoundment with approximately two thirds of its area deeper than 2 m. Although the lake stratified chemically and thermally during the summer, dissolved oxygen generally was >4.0 ppm above the 3-m contour. Ice covered the lake between November 1971 and March 1972.

The lake presently is managed as a public picnicking and fishing area, with largemouth bass and bluegills (*Lepomis macrochirus*) being the only abundant fishes.

Fish were collected from July 1971 to November 1972 with a 230 V alternating current boom electroshocker operated along the shoreline during the day. Bass were taken to shore and measured, tagged, and released. Fish were assigned to age groups by examination of magnified scale impressions. In July and August 1971, a numbered Monel Metal® strap tag (size 1, style 4-1005, National Band and Tag Co.) was attached to the lower jaw of each fish over 100-mm total length (age I and older). Data analyses are restricted to the 1970 year-class.

The April 15 through November 15, 1972, study interval was divided into 14 semimonthly recapture periods, with the convention that an individual fish would be recorded as captured no more than once during each half-month regardless of the number of times it was actually taken in the interval. Approximately five sampling trips consisting of two electrofishing passes around the shoreline were made during each of the half-month periods.

The number of recaptures for each tagged bass collected in 1972 was counted and an observed frequency-of-capture distribution was determined for the 1970 year-class. The agreement between the observed frequencies and those expected from a model allowing mortality and migration between sample periods was used to test assumptions of equal catchability for the tagged population.

Theoretical Framework

Frequency-of-capture data may be used to test the hypothesis of equal catchability throughout the population sampled if an appropriate distribution of capture frequency can be derived. This is an extension of using capture frequencies to estimate population size (Craig 1953; Eberhardt 1969; Edwards and Eberhardt 1967; Leslie 1958; Nixon et al. 1967; Turner 1960). For example, if captures are assumed to occur with constant, equal probability over time, and neither losses nor recruitment take place during the study, individual frequencies of capture would be expected to follow the binomial distribution with parameters n, the number of sampling periods, and p, the proportion of the tagged population caught per period (Eberhardt 1969). The assumptions of this binomial model could be tested for a set of data by estimating n and p and then checking the goodness-of-fit between observed and expected capture frequencies. A poor fit would cause one to question the validity of either or both assumptions used in the model.

This study required a probability distribution of capture frequency that allowed mortality and migration of tagged fish to or from the shoreline during the 1972 study interval. Holgate (1964, 1966) described such a probability distribution to predict frequencies of capture in a population of small mammals open to migration. His model is based upon the concept that the number of times an individual is captured depends not only upon its physical catchability, but also upon its length of residence in the area sampled. Because electrofishing is effective only in shallow water, samples are probably biased if lengths of residence or exposure to sampling at the shoreline vary greatly among individuals in the lake.

If all members of the population are assumed to have equal and constant probability $(1 - k)$ of leaving a study area through emigration or death between two consecutive sampling periods, the number of sample periods of residence (T) follows the geometric distribution (Holgate 1964, 1966)

$$P(T) = (1 - k)\, k^T \quad T = 0, 1, 2, \ldots$$

Because some animals that occupy the study area may not be captured at all and because not all animals are captured during each period, the true periods of residence (T) are unobservable, requiring the distribution of the observed lengths of residence (x) to be conditional upon the animal being captured at least once. This produces a zero-modified geometric model, where

$$P(0) = (1 - k)/(1 - qk)$$
$$P(x) = (1 - q)(1 - k)\, k^x/(1 - qk) \quad x = 1, 2, \ldots$$

and where $(1 - q)$ is the probability of capture during a given sample period (Holgate 1964). The observed length of residence (x) is the number of sampling periods elapsed between initial and final captures of an individual. The event that x equals zero can occur in two ways: 1) an individual is captured only one time or 2) an individual is captured twice, but in consecutive sampling periods.

It is also necessary to describe an appropriate distribution of capture frequency within an individual's estimated residence period. As shown by Eberhardt (1969) and Holgate (1966), frequencies of capture from equally catchable fish should follow the binomial distribution in the absence of mortality. The probabilities $(1 - k)$ and $(1 - q)$ in the modified geometric model account for the

TABLE 1. Bivariate distribution of observed and expected (in parentheses) number of captures for estimated shoreline residence periods in 1972. $\bar{x} = 1.0625$; $\bar{y} = 0.1458$; $z = 0.3333$; $\hat{q} = 0.7898$; $\hat{k} = 0.6951$.

Length of shoreline residence, x	No. captures during residence, y			
	0	1	2	≥3
0	[	32 (32.46)		]
1	5 (4.74)	—	—	—
2	1 (2.60)	2 (0.69)	—	—
3	2 (1.43)	2 (0.76)	0 (0.10)	—
4	1 (0.78)	0 (0.63)	0 (0.17)	0 (0.01)
5	0 (0.43)	0 (0.46)	0 (0.18)	0 (0.03)
6	1 (0.24)	0 (0.31)	0 (0.17)	0 (0.05)
7	0 (0.13)	0 (0.21)	0 (0.14)	0 (0.06)
8	0 (0.07)	0 (0.13)	0 (0.11)	0 (0.06)
9	0 (0.04)	1 (0.08)	1 (0.08)	0 (0.06)
≥10	[	0 (0.59)		]

combined effects of migration and mortality; therefore, the number of captures (y) of an individual during its residence, excluding initial and final captures, should follow the binomial distribution.

$$P(y) = \binom{x-1}{y}(1-q)^y q^{x-y-1}$$

$$x = 1, 2, \ldots \quad y = 0, \ldots, (x-1)$$

with x and $(1-q)$ defined as above.

Finally, the distribution that capture frequencies of all individuals should follow is bivariate, with the number of captures (y) conditional upon the length of residence (x), or

$$P(x=0) = (1-k)/(1-qk) \quad (1)$$

(for $x = 0$, y is undefined)

$$P(x, y) = \binom{x-1}{y}(1-q)^{y+1} q^{x-y-1}(1-k)\, k^x/(1-qk) \quad (2)$$

$$x = 1, 2, \ldots \quad y = 0, \ldots, (x-1)$$

Holgate (1966) gave maximum likelihood estimators of the parameters of the bivariate distribution:

$$\hat{q} = [(\bar{x} - \bar{y} - z)(1 + \bar{y} + z)]/[\bar{x} - (\bar{y} + z)(1 - \bar{x})]$$
$$\hat{k} = [\bar{x} - (\bar{y} + z)(1 - \bar{x})]/[\bar{x}(1 + \bar{y} + z)],$$

where z is the proportion of nonzero x's, $\bar{x}$ is the mean length of residence, and $\bar{y}$ is the mean frequency of capture during residence.

Results

RECAPTURE FREQUENCIES

Numbered tags were placed on 272 of the 1970 year-class largemouth bass in 1971. At tagging, these fish averaged 160-mm total length and 55 g in weight.

In 1972, 48 tagged individuals were captured in the 14 semimonthly sample periods. Of these, 31 were captured once, 11 twice, 5 three times, and 1 fish was captured in four periods, giving 72 captures of 48 fish that were used in tests of catchability. An additional 29 captures of fish that had shed tags were made in 1972. These fish were identified by jaw deformities and scar tissue where tags had been attached, but frequencies of capture could not be determined for these individuals and they have been excluded from further analyses.

TESTS OF CATCHABILITY

The number and timing of captures for each of the 48 tagged fish were used to estimate shoreline residence periods and capture frequencies during residence (Table 1). The mean length of

shoreline residence was 1.06 half-months, and the mean individual capture rate per sample period was 0.15. To test the hypothesis that catchabilities were uniform, expected frequencies for all (x, y) combinations were computed as $48 \cdot P(x, y)$ from equations (1) and (2), and a chi-square statistic was calculated to test the goodness-of-fit between observed frequencies and those expected from the bivariate model. Because expectations for most (x, y) cells were small (Table 1), pooling of the data was required to calculate an appropriate chi-square statistic (Conover 1971). There is no standard statistical procedure for calculating chi-square in a bivariate distribution when individual cells have low expected numbers; however, if the pooling is not done consistently over only one variable, the test should remain sensitive to both variables in the model. Neighboring cells in Table 1 were grouped to produce composite expectations close to or >3.0, and the resultant chi-square statistic, with 3 df, was 4.80 (Table 2, upper half). Thus, the hypothesis that capture frequencies fit the bivariate model, which assumed equal catchability of bass present at the shoreline, could not be rejected ($P > 0.05$). Though this indicates that differences in physical catchability were not detectable for largemouth bass that occupied the shoreline, Parker and Hasler (1959) and Lewis and Flickinger (1967) suggested that shoreline subpopulations constituted only a small portion of the total population during the summer. Consequently, with shoreline electrofishing, bass living offshore may not be equally catchable for behavioral and physical reasons.

This possibility was examined by redefining residence as being present anywhere in the lake and assuming that all individuals had equal probability of being captured. Tagged fish captured anytime in 1972 had to be alive during the first 1972 sample period, April 15–30. Residence times in the lake, therefore, were estimated as the number of half-months between the first sample period in April and the final capture periods, and revised capture frequencies were determined (Table 3).

Estimates of mean length of lake residence and mean frequency of capture were 2.77 half-months and 0.40 captures, respectively. The chi-square goodness-of-fit statistic between observed and expected frequencies with 6 df was 42.54 (Table 2, lower half). Consequently, the hypothesis that capture frequencies of all 1970 year-class bass fit the bivariate model was rejected ($P < 0.01$) even though the same hypothesis was not rejected for shoreline residents. Rejection in this second test resulted from failure of either or both assumptions of the model to hold for the 1970 year-class as a whole, i.e. the probability of capture $(1 - q)$, or the probability of emigration or death $(1 - k)$, was unequal between individuals and/or time varying in 1972. Separate analyses of these two effects are not possible from the frequency-of-capture data alone; however, either failure would produce biased capture frequencies when compared with the shoreline residents. Thus, the tagged 1970 year-class population consisted of two groups: 1) shoreline residents with similar catchabilities and 2) another group whose nonrandom exposure to sampling at the shoreline caused their frequency-of-capture distribution to differ from that of the shoreline fish.

TABLE 2. Groupings of residence times (x) and capture frequencies during residence (y) used to calculate chi-square statistics for shoreline residencies (Table 1) and lake residencies (Table 3). Observed = O; Expected = E.

	Frequencies		
$[x, y]$ Groupings	O	E	$(O - E)^2/E$
Shoreline			
$[x = 0; y$ undefined$]$	32	32.46	0.006
$[x = 1; y = 0]$	5	4.74	0.014
$[x = 2, 3; y = 0]$	3	4.03	0.263
$[x = 2, 3; y = 1, 2]$	4	1.55	3.872
$[x = 4, 5, 6;$ all $y]$	2	3.46	0.616
[all other combinations]	2	1.76	0.033
Total	48	48.00	4.804
Lake			
$[x = 0; y$ undefined$]$	6	21.14	10.843
$[x = 1; y = 0]$	11	5.43	5.714
$[x = 2; y = 0]$	10	2.94	16.954
$[x = 2, 3; y \geq 1]$	4	3.26	0.168
$[x = 3, 4, 5; y = 0]$	5	2.92	1.482
$[x = 4, 5; y \geq 1]$	7	3.62	3.156
$[x = 6 - 10; y = 0, 1]$	3	2.00	0.500
$[x = 6 - 10; y \geq 2]$	2	3.88	0.911
[all other combinations]	0	2.81	2.810
Total	48	48.00	42.538

RECAPTURE TO CAPTURE RATIOS

A plot of the number of tagged recaptures as a proportion of the total catch for each sample period of the study suggested that fish susceptible to capture at the shoreline during the summer constituted a small and variable portion of the total population (Fig. 1). The recapture to capture ratio increased in 1971 because newly tagged fish were continually added to the population, but the ratio should have remained stable thereafter if 1) there was no differential mortality, 2)

TABLE 3. Bivariate distribution of observed and expected (in parentheses) number of captures for estimated lake residence periods in 1972. $\bar{x} = 2.7708$; $\bar{y} = 0.3958$; $z = 0.8750$; $\hat{q} = 0.6784$; $\hat{k} = 0.7980$.

Length of lake residence, x	No. captures during residence, y				
	0	1	2	3	≥4
0	[		6 (21.14)		]
1	11 (5.43)	—	—	—	—
2	10 (2.94)	1 (1.39)	—	—	—
3	3 (1.59)	3 (1.51)	0 (0.36)	—	—
4	1 (0.86)	4 (1.22)	2 (0.58)	0 (0.09)	—
5	1 (0.47)	1 (0.88)	0 (0.63)	0 (0.20)	0 (0.02)
6	0 (0.25)	0 (0.60)	0 (0.57)	0 (0.27)	0 (0.07)
7	0 (0.14)	1 (0.39)	0 (0.46)	0 (0.29)	0 (0.12)
8	2 (0.07)	0 (0.25)	0 (0.35)	0 (0.28)	0 (0.17)
9	0 (0.04)	0 (0.15)	0 (0.25)	0 (0.24)	0 (0.21)
10	0 (0.02)	0 (0.09)	1 (0.18)	1 (0.19)	0 (0.23)
≥11	[		0 (2.81)		]

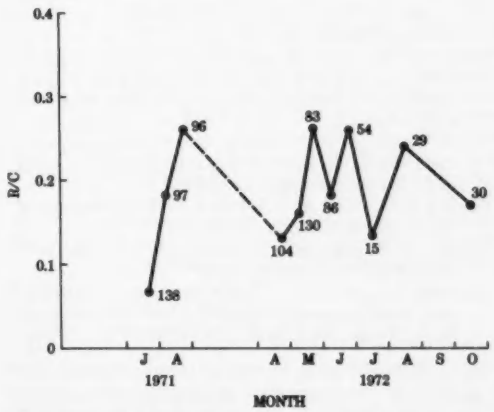

FIG. 1. Recapture to capture ratios of 1970 year-class largemouth bass (*Micropterus salmoides*) in 1971 and 1972. R is the number of tagged recaptures, and the total catch (C) is indicated for each estimate.

marked fish were recognized upon capture, and 3) sampling was random. The low ratios for April and the first half of May are believed the result of movement of a large number of untagged fish to the shoreline, rather than a disproportionate loss of tagged individuals, because the recapture to capture ratios increased after the first half of May (Fig. 1). Although the ratios were quite variable from June 1972 onward, the values approached a level similar to that of the final 1971 sampling period, in spite of some tag loss (Fig. 1). This implies that individual bass retained their habitat preferences from one year to the next and that fish tagged during the summer of 1971 were not random samples from the entire population.

Discussion

The data indicate that behavioral patterns of tagged 1970 year-class largemouth bass influenced catchability with shoreline electrofishing so that midsummer population estimates referred only to the population segment that occupied the shoreline. This is consistent with the results of Lewis and Flickinger (1967) and Parker and Hasler (1959). They found young largemouth bass separated into two subpopulations during the summer, one segment whose individuals occupied home ranges at the shoreline and another segment that occupied offshore waters. Lewis and Flickinger (1967) reported that an average of only

1.2% of the total population was captured during the first electrofishing pass around a 3.4-ha pond, indicating the shoreline group to be small in comparison with the offshore group. This was also illustrated by Lewis et al. (1962), who underestimated a known-size bass population when using electrofishing in a mark and recapture experiment.

Significant intermixing of the two segments apparently occurred during the early spring, yet there was evidence of the year-to-year persistence in summer habitat selection, as shown by the tagged bass in this study and by Lewis and Flickinger (1967).

The statistical tests used in this study were directed only at the tagged portion of the population. Tagging frequently has been shown to alter the behavior of fishes, but it is unlikely that significant, long-range behavioral patterns such as those discussed could be induced only by tagging. The arbitrary pooling of frequency cells prior to calculating the chi-square statistic for the goodness-of-fit tests can produce a variety of chi-square values from a single bivariate table, depending upon the particular pooling criteria and options employed. Several analyses of the data in Tables 1 and 3 were made by pooling different cells to obtain composite expectations approximately equal to 3.0. All tests produced conclusions consistent with those presented in the results. Another potential bias of the data is shown by the 29 recaptures of bass that had lost tags. This represents an approximate 30% [29/(72 + 29)] loss of frequency information about tagged fish taken in 1972. This could affect data interpretation if tag loss was related to behavior or catchability.

Explanation of factors causing, and benefits derived from, behavioral segregation is beyond the object of this paper, but Gerking (1959) has reviewed restricted movement patterns of fish populations. Much evidence suggests that many species of fish have seasonal and/or diel behavioral patterns that affect the randomness of samples from their populations and in turn lead to biased conclusions regarding these populations and their members.

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Effects of Pulpmill Effluent on Phytoplankton Production in Coastal Marine Waters of British Columbia

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STOCKNER, J. G., AND D. D. CLIFF. 1976. Effects of pulpmill effluent on phytoplankton production in coastal marine waters of British Columbia. J. Fish. Res. Board Can. 33: 2433–2442.

Phytoplankton production adjacent to two kraft pulpmills in Howe Sound, British Columbia, was considerably lower than daily rates at control stations removed from the zone of influence. Average daily production at the Port Mellon mill was 29 and 24 mg $C \cdot m^{-2} \cdot day^{-1}$ in 1973 and 1974, in contrast with 332 and 367, in respective years at the control. Less difference in production was seen between Woodfibre mill and its control, because this mill is situated in a more actively flushed location. Howe Sound studies showed little qualitative or quantitative difference between chlorophyll *a* levels or phytoplankton assemblages among mill and control stations. *Skeletonema costatum* and *Thalassiosira* spp. were dominant phytoplankton species. Light attenuation and selective absorption of 400–500 nm wavelength light by kraft mill effluent was considered the major factor responsible for reduced production in the zone of influence. Axenic culture studies with marine phytoplankton showed that phytotoxicity occurs only at high effluent concentrations. Our laboratory experiments suggest that, given sufficient time, it is possible for phytoplankton to adapt to relatively high effluent concentrations, if pH remains normal.

STOCKNER, J. G., AND D. D. CLIFF. 1976. Effects of pulpmill effluent on phytoplankton production in coastal marine waters of British Columbia. J. Fish. Res. Board Can. 33: 2433–2442.

La production de phytoplancton dans le voisinage de deux moulins de pâte à papier kraft dans le détroit de Howe, Colombie-Britannique, est beaucoup plus faible que les taux quotidiens observés à des stations témoins en dehors de la zone d'influence. La production quotidienne moyenne au moulin de Port Mellon était de 29 et 24 mg $C \cdot m^{-2} \cdot jour^{-1}$ en 1973 et 1974, comparativement à 332 et 367 aux stations témoins pour ces deux années respectives. La différence dans la production phytoplanctonique entre le moulin de Woodfibre et son témoin est moindre, parce que ce moulin est situé dans un endroit ou le vidage se fait plus activement. Les études du détroit de Howe révèlent peu de différences qualitatives ou quantitatives entre les niveaux de chlorophylle *a* ou les assemblages phytoplanctoniques parmi les stations du moulin et les stations témoins. *Skeletonema costatum* et *Thalassiosira* spp. sont les espèces dominantes du phytoplancton. On est d'avis que l'atténuation de la lumière et l'absorption sélective de lumière de longueur d'onde de 400–500 nm par l'effluent de papeterie kraft est le principal facteur de la diminution de production dans la zone d'influence. Des expériences de culture axénique de phytoplancton marin démontrent que la phytotoxicité ne se rencontre qu'à de hautes concentrations d'effluent. D'après nos expériences en laboratoire, le phytoplancton pourrait, avec le temps, s'adapter à des concentrations d'effluent relativement élevées si le pH demeurait normal.

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THE environmental effects of pulpmill effluent on marine phytoplankton communities in British Columbia coastal waters are not well understood. Tully (1949), Waldichuk (1954), Sibert and Parker (1972), and Parker and Sibert (1972, 1976) studied effects of kraft mill effluent in Alberni Inlet, B.C. as it relates to depressed oxygen levels, but with the exception of the latter two studies, the effect of light attenuation by pulpmill effluent stain on phytoplankton photosynthesis has been ignored. Practically nothing is known of the potential toxicity of mill effluent to marine algae.

Since April 1972, the plankton ecology group at the Pacific Environment Institute has been interested in the production and distribution of phytoplankton in Howe Sound and the Strait of Georgia. This work has included sampling two stations in Howe Sound located adjacent to two kraft process pulp mills, Woodfibre and Port Mellon. A significant reduction in primary pro-

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duction was noted in water adjacent to these mills, when compared with controls[1] situated a few kilometers removed. Attempts were made from 1973 to 1975 to elucidate by field experiment whether phytotoxicity or light attenuation, or both, were involved in the observed production depression.

This report presents data gathered over a 3-yr period at mill and control stations in Howe Sound and represents over 200 in situ experiments. Supportive information from a cursory examination of an additional six pulp mills situated along the British Columbia coast is also presented, together with results of laboratory work on axenic marine phytoplankton cultures conducted in 1975 to test pulpmill effluent for phytotoxicity.

Materials and Methods

Study Area

Carter (1934) considered Howe Sound to be a combined fjord and coastal embayment, the fjord portion extending from Anvil Island north to the Squamish River estuary (Fig. 1). The Squamish River discharge influences all of Howe Sound, particularly the central channel which includes Areas 5, 2, and 1 (Fig. 1). From May to September, the river carries a heavy glacial silt load which forms an opaque, freshwater lens on the surface of Howe Sound. Because rainfall is heavy (approximately 221 cm annually), and mean river discharge is relatively large (242 $m^3 \cdot s^{-1}$), Howe Sound is considered a positive estuary, where precipitation and runoff greatly exceed evaporation, resulting in a net seaward water flow. A brief description of Howe Sound estuarine circulation is given by Giovando (1972). Although Howe Sound is a multilayered system, it is the surface layers (euphotic zone) that are important in this study.

Stations 3, 4, 6, and 8 were situated in Howe Sound (Fig. 1). Station 4 (depth to bottom from actual water surface, $z = 40$ m) was located approximately 50 m from the acid-sewer discharge at Port Mellon. Station 3 ($z = 150$ m), the control for Station 4, was located 100 m off the southern tip of Woolridge Island, 2 km from Station 4. Station 8 ($z = 65$ m), off Woodfibre, was 50 m east of the Mill Creek discharge. Station 6 ($z = 50$ m), the control for Station 8, was situated on the "sill" at the constriction of Howe Sound, 11 km south of Woodfibre. All stations were sampled monthly commencing in February–March 1973.

In 1973 and 1974 experiments to determine daily production were conducted off six mills located along the British Columbia coast (Stockner et al. 1975). One sample set was incubated in the zone of influence and the control set in an area close to the mill but unaffected by effluent.

[1]The use of the word "control" is arbitrary. There is no ideal "control" situation for Howe Sound stations.

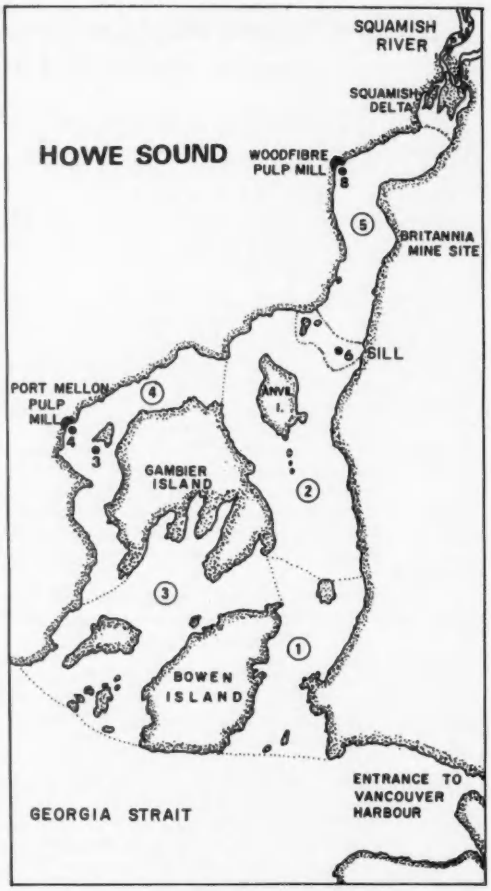


FIG. 1. Howe Sound showing station locations (●) and zones (○) referred to in text.

Physical and Chemical Data

Total incident solar radiation (gram-calories per square centimeter) was recorded on a Belfort pyrheliometer. Extinction of surface light with depth was measured by a Montedoro-Whitney Underwater Illuminance meter (Model LMT-8A). The natural logarithm of light intensity was plotted against depth, and the slope of a straight line fitted to the points by linear regression provided an estimate of the mean downward extinction coefficient. Intensity of surface radiation (in foot-candles) was measured by a Gossen handheld light meter. A standard 30-cm white Secchi disc was used to measure water transparency at every set. In measuring light penetration adjacent to pulp mills, special care had to be taken

to drift onto the station so as not to disturb the surface stain.

Temperature profiles to a depth of 60 m were obtained with a bathythermograph (B.T.). A bucket thermometer was used to measure surface temperatures for B.T. calibration.

Water samples were collected from 1-, 3-, 5-, and 20-m depths and later analyzed for the following parameters: total carbonate carbon, salinity, dissolved oxygen, and nutrient analysis (TNO_3, TPO_4, and SiO_3). Total carbonate carbon was measured using an Orion digital pH meter (Model 801). The method of Strickland and Parsons (1968) was used to determine carbonate alkalinity. However, if after acid titration final pH values fell below 3.00, then the sample analysis was repeated using the APHA et al. (1971) standard titrimetric method. Salinity was analyzed with an Auto-lab salinometer (Model 601) to an accuracy of ±0.5%. Density was computed by nomograph from temperature and salinity records. Dissolved oxygen (samples fixed within an hour of being taken) was determined by use of the Winkler titration method (Strickland and Parsons 1968). Samples for nutrient analysis were immediately frozen, and later analyzed by the Fisheries Operations/Environmental Protection Service analytical laboratories, Pacific Environment Institute, West Vancouver, using the methods as outlined in their manual (Fisheries/EPS 1974).

Biological Data

The standard ^{14}C method, as initially proposed by Steemann-Nielsen (1952), was used, with some minor modifications. Water was collected from surface skim, 0-, 1-, 2-, 3-, 5-, 10-, 20-, and 30-m depths using a 6-liter polyvinylchloride Van Dorn bottle. Productivity bottles (two 125 ml light and one 125 ml dark) were inoculated with 1 ml $NaH^{14}CO_3$ (1 μCi) radioisotope stock using an automatic pipet. For each experiment, the number of disintegrations per minute (dpm) per milliliter was determined by placing 1 ml in each of three scintillation vials. In most cases, samples were incubated for 4–5 h, normally from 0930 to 1430. Water was filtered through 0.45 μm BDH cellulose nitrate filters and placed in 10 ml of a specially prepared toluene-based fluor (POPOP, PPO, 2-ethoxyethanol, and toluene). Samples were analyzed within 24 h for activity in a Packard Tri-Carb Liquid Scintillation Spectrometer (Model 3375). The equation of Strickland (1960) was used to convert dpm's to milligrams of carbon per cubic meter. Profiles were integrated by a Hewlett-Packard Calculator Plotter (Model 9820 A) to give phytoplankton production on an areal basis (milligrams of carbon per square meter per day). This involved linear interpolation between data points to the depths where light and dark uptake were equal.

Detailed examination was made of phytoplankton samples from 1- and 5-m depths to assess: a) species composition and b) phytoplankton volumes during key spring and fall bloom periods. Phytoplankton samples were preserved in Lugol's solution and enumerated, using the Utermöhl (1958) sedimentation method. Volumes were determined by equating phytoplankton cells to known geometric shapes. Each phytoplankton sample was examined under 175 and 700 × magnification using a Wild M40 inverted plankton miscroscope. Results were expressed as cells and total volume per cubic meter.

One liter of sea water was taken for chlorophyll *a* analysis from 1-, 3-, 5-, and 20-m depths, and filtered onto Whatman GF/C glass fiber filters with a small amount of $MgCO_3$ added to prevent acidification of filters on freezing. Filters were macerated in a tissue grinder with 10 ml of 90% acetone, and the filtrate analyzed on a Cary recording spectrophotometer (Model 15). The equation of Strickland and Parsons (1968) was used to calculate chlorophyll *a*.

During monthly cruises to Port Mellon, daily areal production was obtained at Station 4 (directly in front of the mill) and at Station 3 (the control, 2 km east of the mill) (Fig. 1). On five occasions, special light experiments were run which differed from the aforementioned in the following way: two sets of ^{14}C incubation bottles (four light, two dark) were filled at each station, one set (two light, one dark) was incubated in situ at the normal location; the other was incubated at the other station. This meant that for Station 3, one set received normal light during incubation, while the second set received strongly attenuated light under the effluent stain. The reverse situation occurred at Station 4, where one set was in its normal location under the stain, while the other was brought to Station 3 and received normal light.

A series of axenic phytoplankton bioassays was conducted using mill effluent from the British Columbia Forest Products pulp mill at Crofton, B.C. Methods used are as described by Stockner and Costella (1976) and Antia and Cheng (1975). Fresh whole mill effluent was filtered through a sterile, enclosed 0.20 μm plain membrane filter unit (Nalgene 120) and added to autoclaved seawater media. Cells were enumerated daily using a Spencer Bright-Line hemacytometer under 200 × magnification. *Skeletonema costatum* and *Dunaliella tertiolecta* came from Dr N. Antia's axenic marine algal culture collection. (*Skeletonema costatum*: clone *Skel* from culture collection of Woods Hole Oceanographic Institution; isolated by R. R. L. Guillard from Long Island Sound, New York. *Dunaliella tertiolecta*: clone *Dun* from culture collection of Woods Hole Oceanographic Institution; isolation details unknown.)

Results

Physical–Chemical Parameters

During winter months, waters are relatively uniform and stable with depth over the whole of Howe Sound. Temperature, salinity, density (σ_T), dissolved oxygen, and inorganic carbonate carbon levels remain constant at all depths and in all areas, except during the infrequent winter freshet periods. From April to October, strong stratification occurs and surface waters are affected by the

heavy discharge of fresh water from the Squamish, and, to a lesser extent, from the Fraser River.

Stations 3 and 4, somewhat removed from the major surface outflow, are less affected by the Squamish River. In early April, a shallow surface layer develops which by June extends to a depth of 5–6 m. This layer is characterized by warm temperatures (11.0–17.0 C), moderate salinity (10.0–24.0‰), density, σ_T (5.0–20.0), carbonate carbon (8,000–23,000 mg C·liter^{-1}) and dissolved oxygen levels (6.0–10.5 mg O_2·liter^{-1}). Underlying this layer is a more dense, saline, cold-water mass with properties characteristic of deep water in the Strait of Georgia (Waldichuk 1957). Total phosphorus and silicate concentrations in the upper zone showed no clear seasonal trends and did not limit phytoplankton production. Total nitrate concentration reached undetectable levels associated with depletion by the vernal phytoplankton bloom in April–May (Stockner et al. 1975). Values in the surface layer remained low until restored to winter levels by complete vertical mixing in November. At Station 4 a surface layer of pulpmill effluent, varying in depth from 0.5 to 1.0 m, occurs throughout the year and is carried several kilometers north and south of the mill before it is thoroughly mixed into the upper zone by wind and tide.

At Stations 6 and 8, a thin (0.5–1.5 m) surface freshwater layer moving seaward exists from May to September, characterized by low temperature, salinity, density, and inorganic carbonate levels. Beneath this layer is a second layer of greater density and higher temperature, similar in properties to the summer surface layer just described for Stations 3 and 4. Beneath this second warmer layer is the cold, dense, saline layer moving slowly up the inlet. This multilayered system is spatially variable and becomes less distinct at Station 6 as the freshwater lens is entrained into the subsurface layer.

Although there is an obvious surface layer of effluent surrounding and extending about 0.5 km north and south of the mill, combined action of wind and tide quickly mixes the effluent into the surface freshwater layer.

Total phosphate and silicate values in the subsurface layer remained relatively high throughout the summer months, but total nitrate showed distinct seasonal variation, reaching low levels at times of peak phytoplankton biomass (Stockner et al. 1975).

Total solar radiation showed typical temperate latitude seasonal variation, but adjacent to the mills, intensity was often reduced by haze from stack emissions.

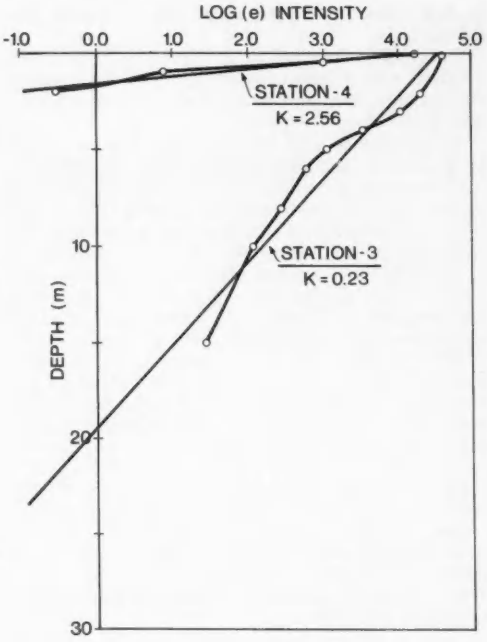


FIG. 2. Plot of light extinction coefficients (k) with depth on August 22, 1974 at Stations 3 and 4 in Howe Sound.

Attenuating properties of surface waters at control stations varied seasonally, being most affected by turbid Squamish and Fraser River water in summer months. At mill stations, effluent stain restricted light penetration to only the top few meters (Fig. 2). The stain affected not only the quantity of light with depth but also its spectral characteristics, strongly absorbing 400–500 nm wavelengths (Fig. 3). Differences in light climate between mill and control stations over a 2-yr period are summarized in Table 1.

BIOLOGICAL PARAMETERS

Phytoplankton assemblages consisted of diatoms, dinoflagellates, cryptophytes, chrysophytes, and euglenoids, with diatoms dominant in number and volume. There was little spatial or temporal variation in the composition of phytoplankton assemblages between mill and control stations, except that dinoflagellates were often more abundant at Stations 3 and 4 than at 6 and 8. *Skeletonema costatum* and *Thalassiosira* spp. were dominant spring bloom species at all stations (Table 1).

Seasonal variation in numbers and volume at

TABLE 1. Annual mean values of selected physical and biological variables at Stations 3, 4, 6 and 8, Howe Sound for 1973 and 1974.

Station	Date	Extinction coefficient (k)	Secchi (m)	Chl a ($mg \cdot m^{-3}$)	Primary production ($mg\ C \cdot m^{-2} \cdot day^{-1}$)	Phytoplankton vol ($mm^3 \cdot m^{-3}$)	Phytoplankton no. ($cells \times 10^6 \cdot m^{-3}$)
3	1973[a]	0.419	5.1	1.34[b]	332	1473	719
	1974[c]	0.380	5.8	1.22	367	3615	2886
4	1973[a]	1.649	2.9	1.13	29	1124	696
	1974[b]	2.368	1.0	0.95	24	2898	3477
6	1973[d]	0.408	4.2	1.08	297	2895	567
	1974[b]	0.495	4.3	0.86	149	2847	3078
8	1973[d]	0.995	1.9	1.21	236	2556	2382
	1974[b]	1.705	1.3	0.44[e]	107	166[e]	277[e]

[a] *Thalassiosira* spp. (spring dominant, all stations).
[b] 0–5 m.
[c] *Skeletonema costatum* (spring dominant, all stations).
[d] *Thalassiosira pacifica* (spring dominant, all stations).
[e] Critical spring bloom sample missing.

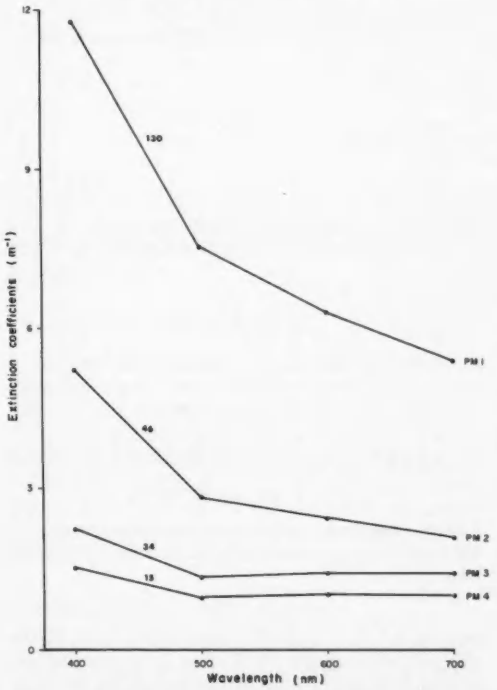


FIG. 3. Absorption of light by three concentrations of kraft mill effluent in the zone of influence (stain gradient) off Station 4 in Howe Sound. (Number on line = apparent color, PM 1–4 = Port Mellon station numbers for special experiment.)

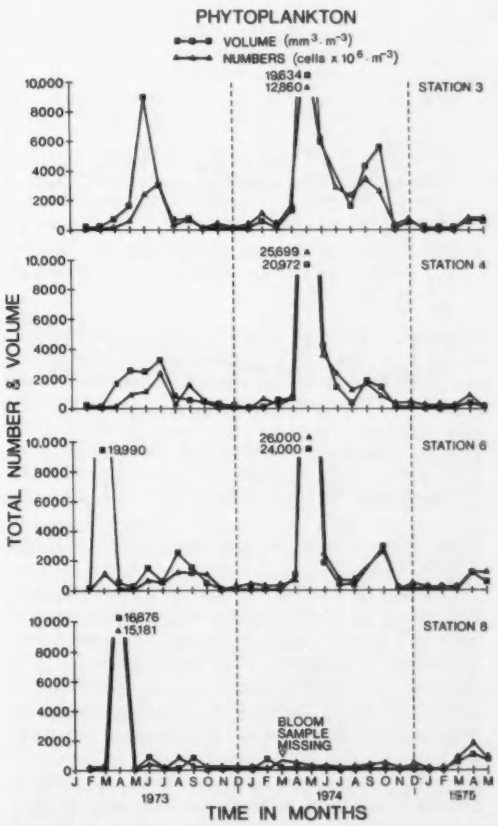


FIG. 4. Phytoplankton biomass and numbers in 1973 and 1974 at 1-m depth at Stations 3, 4, 6, and 8 in Howe Sound.

1-m depth in 1973 and 1974 was similar for all stations, except that no accessory midsummer or autumnal peaks were noted at Stations 6 and 8 (Fig. 4). Annual mean values of phytoplankton numbers and volume serve to illustrate the similarity in phytoplankton biomass among stations (Table 1).

Chlorophyll a values at all stations showed good positive correlation with phytoplankton biomass (Fig. 5). Mean annual values for 1973 and 1974 were, with the exception of Stations 6 and

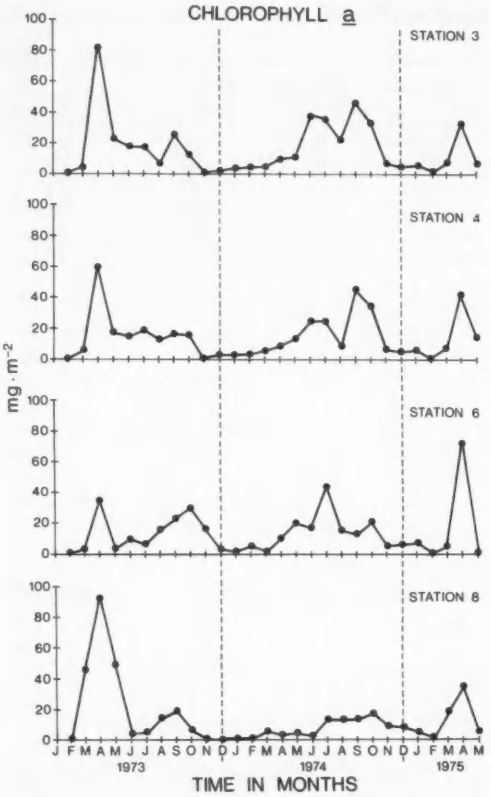

CHLOROPHYLL a
STATION 3
STATION 4
STATION 6
STATION 8
mg · m⁻²
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M
1973
1974
1975
TIME IN MONTHS

FIG. 5. Seasonal abundance of chlorophyll *a* in 1973 and 1974 at Stations 3, 4, 6, and 8 in Howe Sound. Integrated value from surface to 25 m.

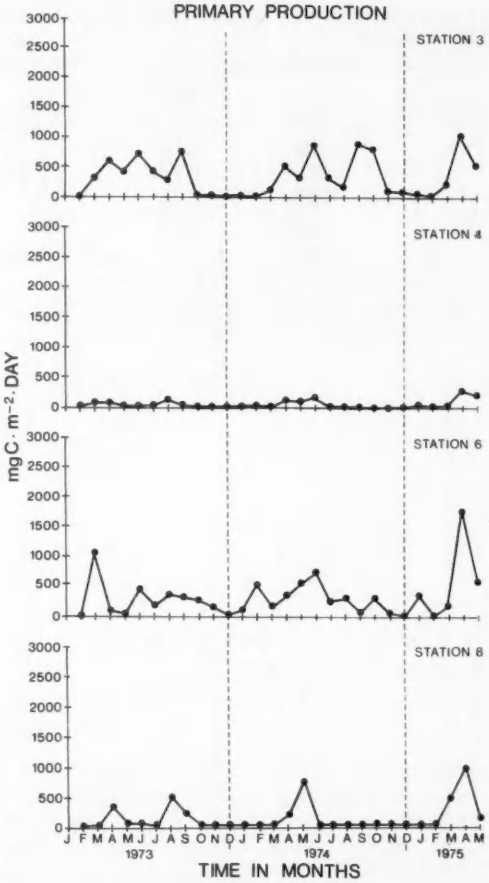

PRIMARY PRODUCTION
STATION 3
STATION 4
STATION 6
STATION 8
mgC · m⁻² · DAY
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M
1973
1974
1975
TIME IN MONTHS

FIG. 6. Seasonal variation of primary production in 1973 and 1974 at Stations 3, 4, 6, and 8 in Howe Sound.

8 in 1974, similar for mill and control stations (Table 1).

Despite similarities in plankton biomass and chlorophyll *a*, mean carbon assimilation rates at Station 3 were an order of magnitude greater than at Station 4, adjacent to the mill (Table 1). The seasonal production curve at the control was similar to many stations in Howe Sound, with pronounced spring and fall peaks, while the curve adjacent to the mills was consistently low and showed no seasonal pattern (Fig. 6). Mean annual production at Station 6 was only slightly greater in both years than mean values at Woodfibre (Station 8).

Figure 7 illustrates results obtained from special light experiments. Detailed results from several experiments are reported in Stockner et al. (1975). When one control set was incubated beneath the stain gradient at Station 4, a significant decrease in production rate occurred. Conversely, when a set from water taken beneath the effluent was brought to Station 3 for incubation, production increased. Of interest is the production–depth profile when the mill samples are incubated at the control. Most of the increase is noted in subsurface layers free of the mill effluent.

In 1975, the pulp mills in British Columbia were closed from July to October. Annual mean areal production adjacent to Port Mellon pulp mill in 1973 and 1974 was 20 and 24 mg $C \cdot m^{-2} \cdot day^{-1}$, in respective years (Table 1). After 14 days without effluent, production increased to 497, nearly doubling again to 810 mg $C \cdot m^{-2} \cdot day^{-1}$ after 35 days (Fig. 8). Such delay in restoration of production was attributable to the continual release of H_2S from sediments.

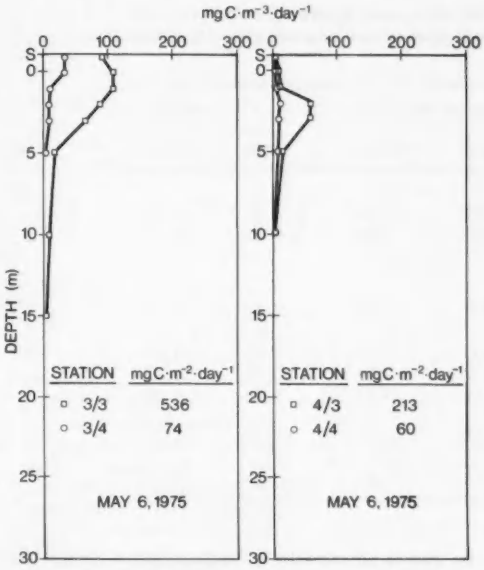
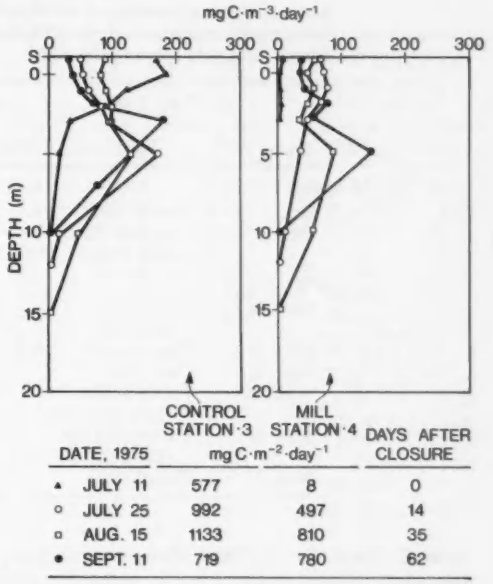


FIG. 7. Cross incubation experiments (primary production) between Stations 3 and 4 on May 6, 1975 in Howe Sound.



DATE, 1975	mg C·m⁻²·day⁻¹		DAYS AFTER CLOSURE
▲ JULY 11	577	8	0
○ JULY 25	992	497	14
□ AUG. 15	1133	810	35
● SEPT. 11	719	780	62

FIG. 8. Primary production at Stations 3 and 4 following pulpmill closure on July 11, 1975.

SPECIAL FIELD EXPERIMENTS

In two experiments conducted in 1975 off Woodfibre and Port Mellon a significant positive relation was shown between subsurface light (k) and phytoplankton production at two depths across an effluent concentration gradient ($R^2 > 0.95$) (Stockner et al. 1975). In the same experiments, light data results demonstrated the strong attenuating properties of concentrated effluent, notably in the 400–500 nm wavelengths (Fig. 3).

AXENIC BIOASSAY EXPERIMENTS

Axenic cultures of marine phytoplankton were used to assess potential growth inhibition (toxicity). Experiments with *Skeletonema costatum* showed normal exponential growth after a 12-day adaptation period in 30% kraft mill effluent. Higher concentrations prevented exponential growth but did not lyse or kill cells (Stockner and Costella 1976). The green alga *Dunaliella tertiolecta* showed normal exponential growth without preadaptation at 80% kraft mill effluent.

Discussion

In a cursory survey of primary production off eight coastal mills (Table 2), two types of responses were noted: a) a significant reduction in phytoplankton production in the zone of influence relative to a clean-water control and b) little or no difference in production between mill and control stations. The mills were, with one exception, kraft process mills so it was unlikely that effluents differed appreciably. Obviously, location was of paramount importance. Adjacent to mills where there was good flushing, phytoplankton production was reduced but little affected by effluent. However, adjacent to mills where flushing was poor, phytoplankton production was severely reduced. Rainville et al. (1975) noted similar results and stressed the importance of flushing.

At mills located in areas where flushing is poor, primary production can be affected in two ways: a) by light attenuation from effluent color and b) by phytotoxicity or physiological stress induced by components in the effluent. Regardless of pathway, the net effect is a reduction in phytoplankton growth in waters adjacent to poorly flushed mills.

Results from field experiments showed light to be the major factor affecting growth (Fig. 7). The strong attenuating properties of pulpmill effluent in sea water have been amply demonstrated by our work and by the studies of Parker and Sibert (1972). Special field experiments off Woodfibre and Port Mellon have shown that as light attenuation (k) decreased, production in-

TABLE 2. Primary production (milligrams of carbon per square meter per day) and chlorophyll (milligrams of chlorophyll *a* per cubic meter) concentrations at several British Columbia coastal pulp mills.

Date	Location	Primary production		Chlorophyll	
		Mill	Control	Mill	Control
1973					
Oct. 2	Powell River	762	1,125	2.05	2.69
Oct. 3	Campbell River (Elk Falls)	357	205	0.69	0.40
1974					
Sept. 20	Nanaimo (Harmac)	1,958	1,920	2.69	1.42
Sept. 21	Port Alberni	160	313	0.82	1.60
Sept. 22	Port Alice	119	721	0.21	1.12
Sept. 24	Prince Rupert (Port Edward)	34	136	1.39	0.82
Sept. 26	Campbell River (Elk Falls)	1,269	1,489	1.48	2.51
Sept. 27	Powell River	49	450	0.24	0.61

creased. Since, in the Port Mellon experiment, laboratory axenic cultures of *S. costatum* were used and temperature differences between laboratory and field were negligible, the importance of adequate light for phytoplankton growth was demonstrated.

Phytoplankton are affected not only by quantity but also quality of light. When the absorption spectra for phytoplankton are compared with absorbance curves for various concentrations of effluent, the strong absorbance of blue light (400–500 nm) coincides with one of two absorbance peaks for chlorophyll *a* and most peaks of accessory pigments. Thus, where effluent color persists (poorly flushed regions), this selective absorption of light is the major factor responsible for the reduction of photosynthesis within the zone of influence.

The closure of all British Columbia pulp mills in the summer of 1975, accompanied by cessation of effluent discharge, demonstrated the rapidity with which phytoplankton production can be restored in waters adjacent to pulp mills once the pollutant is removed and subsurface light conditions improve (Fig. 8). From the evidence presented, one can postulate that as phytoplankton encounter pulpmill effluent and reduced light, most become metabolically inactive and remain quiescent until light conditions improve, i.e. wind and tide disperse the effluent and move them out of the zone of influence.

If the cause of reduced phytoplankton production were related mainly to toxicity, then a significant reduction of phytoplankton biomass and/or an altered community structure should occur in waters affected by effluent. Such a change has not been observed in Howe Sound; instead our results show similar phytoplankton and chlorophyll *a* levels at mill and control stations (Fig. 4 and 5), thereby emphasizing the significance of light rather than toxicity.

Axenic cultures of *S. costatum*, one of the dominant diatoms in British Columbia coastal waters, show normal growth in media containing 30% fresh kraft mill effluent. These studies also demonstrated the ability of phytoplankton to adapt to effluent given sufficient time (Stockner and Costella 1976). In another experiment the marine green alga *Dunaliella tertiolecta* showed normal exponential growth with no lag period in 80% kraft mill effluent (Stockner and Costella 1976). In a study by Rainville et al. (1975), little toxicity was found when *Coccochloris elebans*, was exposed to kraft effluent discharged from three pulpmill biobasins in the southern United States. These results show that algae are capable of adapting to relatively high concentrations of pulpmill effluent and may be the trophic level least affected by effluent discharge in coastal marine waters.

Apparently, we are dealing more with an adaptation problem than phytotoxicity. Further work by Stockner and Costella (1976) directly substantiates the conclusion of this report that the greatest factor influencing primary production is light attenuation by pulpmill effluent. That certain species of phytoplankton are under physiological stress upon exposure to high concentrations of effluent cannot be discounted; however, in a natural assemblage when the pollutant persists

TABLE 3. Annual production in Howe Sound by zone. (See Fig. 1.)

Zone	Area (km^2)	Areal production ($kg\ C \cdot m^{-2} \cdot yr^{-1}$) 1973	Areal production ($kg\ C \cdot m^{-2} \cdot yr^{-1}$) 1974	Zonal production (*metric tons* × $10^3 \cdot yr^{-1}$) 1973	Zonal production (*metric tons* × $10^3 \cdot yr^{-1}$) 1974
1	29.3	0.316	0.512	9.25	14.99
2	43.9	0.140	0.183	6.15	8.03
3	44.5	0.235	0.440	10.46	19.59
4	17.9	0.113	0.127	2.03	2.28
5	21.4	0.081	0.090	1.74	1.93
Port Mellon	6.3	0.012	0.009	0.07	0.06
Woodfibre	6.3	0.044	0.038	0.28	0.24
Total	169.6			29.98	47.12
Production					
in Zone 4 without mill				2.74	3.08
in Zone 5 without mill				2.24	2.49
in Zone 4 with mill				2.03	2.28
in Zone 5 with mill				1.74	1.93
loss in Zone 4 attributable to mill				0.71	0.80
loss in Zone 5 attributable to mill				0.50	0.56
% loss					
in production in Zone 4				26	26
in production in Zone 5				22	22
in production in Howe Sound attributable to both mills				4	3

over long periods, hardier species will replace less resistant ones. Even though phytoplankton could compensate in this way, severe depression of areal production will still result because of the altered light climate, and we doubt whether contact times are of sufficient duration in tidal waters to affect species succession. A change of dominant species did occur between 1973 and 1974 (Table 1) but we feel that such change is not related to mill effluent, but rather to annual variations of physical and chemical parameters.

EUTROPHICATION

Eutrophication (nutrient enrichment) adjacent to mills may in certain situations be a positive attribute, balancing the negative effects of light reduction and toxicity. The increased load of nitrogen and phosphorus compounds, and especially carbon (wood sugars) provide ample nutrients to enhance phytoplankton growth, given sufficient light (Stockner and Costella 1976). Bacterial activity (heterotrophic uptake) is noticeably higher in waters adjacent to mills, and this energy source may in turn enter and enhance the food chain (Sibert and Brown 1975). In several experiments Stockner and Costella (1976) have observed greater growth of test algae in 80% mill effluent than in controls with 80% filtered sea water. The prolific growth of benthic algae at the head of Neroutsos Inlet on Vancouver Island is likely caused by nutrients (mainly nitrogen compounds from the ammonia base) from the Port Alice sulfite mill. Similar observations by others of eutrophication of coastal waters around pulp mills are likely attributable to nutrients in effluents.

IMPACT ASSESSMENT — HOWE SOUND

In addition to cause and effect studies, it is of interest to assess the impact such waste discharge has on the annual production of carbon in Howe Sound. Such estimates provide some basis for judging environmental costs of effluent disposal from mills operating on the coast.

If no mills were situated in Howe Sound, total carbon production in 1973 and 1974 would have been approximately 30 and 48 metric $tons \cdot yr^{-1}$, respectively. The operation of the mills reduces this Howe Sound total by about 2 to 4%, depending on the year (Table 3). However, in a given region (zone) the effect is considerably greater, 26 and 22% in zones 4 and 5, respectively, assuming that mill influence extends for a 2-km radius.

Caution must be invoked when using these data to interpret environmental impact. First, though the effect on primary production appears localized, effects on more sensitive invertebrate

larvae and zooplankton may be substantial (Klimashauskene 1973). We have observed many herring and juvenile salmonids apparently stunned by pockets of high concentration effluent. Also diminishment of primary production, the base of the food web, possibly by as much as 25%, will affect higher trophic levels and reduce the biological carrying capacity of a body of water.

Acknowledgments

We thank the officers and crew of C.F.A.V. *Endeavor* and *Laymore* and Dr I. H. Rogers and Messrs K. Shortreed, D. Buchanan, and S. Matheson for field assistance. We are grateful to Ms K. Munro for phytoplankton enumeration and data collation, and to Ms A. Costella who performed the axenic culture work. Special thanks are extended to Drs M. Waldichuk and N. Antia for critical review of the manuscript. Dr Antia provided assistance in initial phases of the axenic work and provided test species from his culture collection. We are grateful to Environmental Protection Service, Environment Canada, for providing funds to support the axenic culture work.

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Effects of Dry Pellet Diets on the Metabolic Rates of Bluegill (*Lepomis macrochirus*)[1]

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SCHALLES, J. F., AND T. E. WISSING. 1976. Effects of dry pellet diets on the metabolic rates of bluegill (*Lepomis macrochirus*). J. Fish. Res. Board Can. 33: 2443–2449.

Experiments were designed to evaluate the effects of five dry pellet diets containing various protein levels on metabolic rates and energy cost of food utilization of bluegill (*Lepomis macrochirus*). In the 48-h period after feeding metabolic rates increased an average of 57% above base levels established prior to food presentation. The energy cost of food utilization, estimated as a percentage of ingested food energy, was $\bar{x}$ 14.90 ± 0.96% SE (range 7.5–32.3%). Positive correlation was found between protein and caloric intakes and the increases in O_2 consumption observed after feeding. Percent protein in the diet had no significant effect on mean values of O_2 consumption after feeding or the estimates of the energy cost of food utilization. Probably the calorigenic effect of protein in fishes, which are principally ammonotelic, is considerably lower than that observed in ureotelic and uricotelic vertebrates. The mean estimate (14.90% of ingested energy) for the bluegill could reflect a low specific dynamic action of protein in conjunction with the calorigenic effect of the carbohydrate and lipid components of the diets.

SCHALLES, J. F., AND T. E. WISSING. 1976. Effects of dry pellet diets on the metabolic rates of bluegill (*Lepomis macrochirus*). J. Fish. Res. Board Can. 33: 2443–2449.

Les auteurs ont poursuivi des expériences dans le but d'évaluer les effets de cinq régimes de boulettes sèches contenant divers niveaux de protéines sur le taux métabolique et le coût énergétique de l'utilisation de la nourriture chez des crapets arlequins (*Lepomis macrochirus*). Durant les 48 h qui suivent le repas, les taux métaboliques augmentent de 57% en moyenne au-dessus des niveaux de base établis avant présentation de la nourriture. Le coût énergétique de l'utilisation de la nourriture, estimé en pourcentage de l'énergie de la nourriture absorbée, est de $\bar{x}$ 14.90 ± 0.96 é.t. (extrêmes 7.5–32.3%). Il y a corrélation positive entre les protéines et les calories absorbées d'une part et l'augmentation d'O_2 consommé après le repas d'autre part. Le pourcentage de protéines dans le régime n'a pas d'effet significatif sur la consommation moyenne d'O_2 après le repas, ou sur les estimés du coût énergétique de l'utilisation de la nourriture. Il est plus probable que l'effet calorigène des protéines chez les poissons, qui sont surtout amonotéliques, est considérablement plus faible que celui que l'on observe chez les vertébrés uréotéliques et uricotéliques. L'estimé moyen (14.90% de l'énergie absorbée) obtenu pour le crapet arlequin peut refléter une faible action dynamique spécifique des protéines, couplée à l'effet calorigène des hydrates de carbone et des lipides des régimes.

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AN increase in the rate of O_2 consumption in fish subsequent to the feeding of natural food items has been reported by a number of investigators (Saunders 1963; Livingston 1968; Kausch 1969; Wissing and Hasler 1971; Muir and Niimi 1972; Solomon and Brafield 1972; Hamada and Ida 1973; Pierce and Wissing 1974; Beamish 1974). This phenomenon is often referred to as the specific dynamic action (SDA) of feeding and to a large extent reflects the energy cost of food utilization. A number of physiological events appear to contribute to this elevation of metabolic rate after feeding. These include digestion and assimilation, protein catabolism, urea formation and excretion, ATP synthesis, protein synthesis, and caloric homeostatic mechanisms (Warren 1971; Schalles 1973).

The present study was designed to compare the effects of dry pellet diets on the metabolic rates of bluegill (*Lepomis macrochirus*) with those observed in an earlier study of the same species fed ad lib. on live mayfly nymphs (Pierce and

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Wissing 1974). The level of protein in the experimental diets was also varied to examine the extent of protein SDA in the bluegill, which is principally ammonotelic.

Materials and Methods

Bluegill were obtained by hook and line from a private pond in Preble County, Ohio. Initially, groups of five to seven fish were introduced into 130-liter aquaria. Fish that readily accepted food were moved to separate, 40-liter compartments for the remainder of the holding period and were conditioned to feed in isolation.

All experimental fish were maintained on a conditioning regimen for a minimum of 6 wk prior to their use in the respirometer. The fish were fed a commercial diet (Strike Fish Pellets, Agway Inc.) daily and held at ambient room temperature (22–24 C) under a 16 h L:8 h D photoperiod.

A detailed description of the respirometer is given in Pierce and Wissing (1974). Briefly, the respirometer consists of a 6.15-liter plexiglass holding chamber supplied with a continuous flow of filtered, aerated water. For determination of O_2 consumption, flow is diverted from a chamber used for aeration and filtration, thus creating a closed system within which changes in pO_2 are measured by an oxygen electrode and gas monitor connected to a potentiometric recorder. The system was automated for the present study by installing solenoid valves to divert flow during measurements of O_2 consumption. The solenoid valves and the recorder were actuated by an automatic timer.

Trials were carried out during the period of November 1972–July 1973. Data were collected on six fish. Each fish was fed on the day preceding introduction into the respirometer. In each trial a fish was weighed and placed in the respirometer for 17 days, during which five experimental diets were fed randomly. Respiration was measured at 2-h intervals throughout each trial. Water temperature was maintained at 25 ± 0.5 C.

The experimental day began at 0800 on one day and extended to 0800 of the following morning. Day 1 of each trial was considered a period of conditioning to the respirometer. Measurements of O_2 consumption on day 2 were used to compute the first set of unfed, routine metabolic rates. Day 3 was the first day of feeding. Food pellets were offered ad lib. in feedings at 0900 and 1900. Two days were then allowed for metabolic rates to return to prefeeding levels. Day 5 metabolic rates were used as the next set of prefeeding rates. The fish was fed a second diet on day 6. For these and subsequent feedings the fish was given the same ration as had been consumed on day 3, to allow for better comparisons of metabolic response to the different diets. The fish was fed the remainder of the diets on days 9, 12, and 15. For all experiments the day of feeding will be referred to below as F1 and the day subsequent to feeding as F2. The second day after feeding, when the next set of prefeeding metabolic rates was determined, will be referred to as PF.

At the end of each trial the fish was removed from the respirometer holding chamber and weighed. Pretrial and posttrial weights were averaged to determine the experimental weight used in the calculations of metabolic rates. In five of the six trials water was returned to the holding chamber after removal of the fish, and measurements of O_2 consumption were continued as a check on the biological oxygen demand (BOD) in the system. Analysis of BOD showed that this factor accounted for an average of 5.0% (range 2.5–8.3%) of the O_2 consumption for the final day of the trial. Because BOD would accumulate gradually to these levels, no correction was made for this factor.

The five experimental diets were formulated at the Federal Fish Farming Experimental Station, Stuttgart, Arkansas. The objective of the formulations was to obtain diets of varying protein level with balanced amino acid composition, similar caloric contents, and similar amounts of fat and fiber. To this end, a high protein mix containing soybean meal (40%), fish meal (15%), poultry by-product (15%), feather meal (10%), distillers solubles (15%), and delactosed whey (5%) was combined in varying proportions with a low protein formulation containing ground soft winter wheat with lysine and methionine supplements. The ratios of combination for diets A through E (high protein to low protein) were 0.2:0.8, 0.32:0.68, 0.45:0.55, 0.7:0.3, and 1.0:0.0, respectively. A standard vitamin premix was added to the formulations. Diets were packaged in a pellet of 3.2 mm in diameter and 3.2–6.4 mm long. Pellets were subsequently trimmed to about 1.6 mm in length, a size more readily accepted by the fish.

Results of the proximate analyses are given in Table 1. Dry weights of the pellets were determined by drying at 105 C to constant weight. Percent organic matter was determined by ashing samples at 550 C to constant weight. Caloric values were obtained by averaging replicate values obtained with a Phillipson microbomb calorimeter (Phillipson 1964). Protein nitrogen was determined with the standard Kjeldahl technique, and a conversion factor of 6.25 g protein/g N was used in the calculations. Crude fat and fiber were estimated from a standard feedstuffs table (Hubbell 1970).

Measurements of O_2 consumption, in millimeters Hg per minute, were converted to milligrams O_2 per kilogram-hour with the equation of Pierce et al. (1973). Caloric equivalents of the metabolic rates were then calculated with an oxycaloric coefficient of 3.42 cal produced/mg O_2 consumed (Brody 1945). Estimates of the energy cost of food utilization were calculated as the average of days F1 and F2 metabolism minus the PF metabolism and expressed as a proportion of ingested energy.

An analysis of variance program for randomized block design (APL Statpack 1; Smillie 1968) was used to test for significant differences among the diet responses for the increased metabolic rates subsequent to feeding and the estimates of the energy cost

TABLE 1. Composition of the five experimental diets fed randomly to six bluegill (*Lepomis macrochirus*).

Diet	Moisture content (%)	Organic content (% *dry wt*)	Crude protein content (% *dry wt*)	Crude fat content (% *dry wt*)	Crude fiber content (% *dry wt*)	Gross energy (*kcal/g dry wt*)
A	7.7	86.4	23.9	4.6	9.4	3.88
B	7.8	85.8	26.6	4.6	8.6	3.92
C	8.0	85.2	30.6	4.7	7.8	3.96
D	7.8	84.1	36.1	4.8	6.2	4.06
E	7.3	83.0	45.3	4.9	4.4	4.28

TABLE 2. Food intake, as percent wet body weight, for the six experimental bluegill fed diets A–E at 25 C.

Fish no.	Wet body wt (*g*)	Diet				
		A	B	C	D	E
1	60.5	1.98	1.98	1.98	1.98	1.98
2	68.7	1.65	1.65	1.65	1.65	1.65
3	73.1	1.94	1.94	1.94	1.52	1.94
4	75.7	1.43	1.43	1.43	1.43	1.43
5	85.0	2.17	2.61	2.61	2.52	2.04
6	74.1	1.67	1.51	1.67	1.67	1.67

of food utilization. A simple linear regression analysis was used to examine for possible relationships of protein and caloric intakes to the increases in rates of O_2 consumption after feeding and to the energy cost of food utilization. To account for the possible influence of qualitative differences in the diet responses on the above regressions, a "dummy" variable multiple regression analysis was employed (Draper and Smith 1966).

Results

Food ingested, as percent wet body weight, is given in Table 2. For all trials the average intake was 1.83% (range 1.43–2.16%). In general, the levels of food intake established on day 2 of the trials were replicated for subsequent feedings.

Average hourly rates of O_2 consumption for each day of the trials are shown in Table 3. Random order of diet presentation is shown in parentheses. Usually the prefeeding rates (PF) were similar throughout each trial. However, for three fish (fish 1, diet B; fish 3, diet A; and fish 5, diet B) rates of O_2 consumption for day 2 of the trial were markedly lower than subsequent PF rates. A large difference exists between the pre- and postfeeding rates for fish 1, diet B. During regression analysis estimates based on the data for this fish were found to be statistical outliers (Snedecor and Cochran 1972).

There was always an appreciable increase in metabolic rate after feeding. For all trials the metabolic rates were elevated by an average of 57% above prefeeding rates for the 48-h period subsequent to the 0900 feedings. Paired *t*-tests established that all rates of O_2 consumption for F1 days differed significantly from PF rates ($P < 0.01$). For diets A through E the mean increases in O_2 consumption for the 48-h period subsequent to feeding were 48.9, 67.3, 55.8, 52.1, and 68.1 mg/kg-h, respectively.

Hourly values of all PF, F1, and F2 days were averaged for each fish to obtain a general picture of the metabolic response to the feeding of the dry pellet diets. The average caloric expenditures obtained for each 2-h interval are shown in Fig. 1. Both feedings resulted in increased metabolic rates. Maximum rates were observed generally between 2000 and 0200 of F1 days. Metabolic rates declined gradually after the maximum rates were reached and had returned to prefeeding levels within 48 h after feeding. Graphically, the energy cost of food utilization may be regarded as the area of the curve that is bounded by the dashed line representing the average PF rate and the line for the metabolic rates of F1 and F2 days.

Estimates of the energy cost of food utilization are given in Table 4. Mean values are presented

TABLE 3. Average hourly rates of oxygen consumption by bluegill (milligrams of O_2 per kilogram-hour) for day prior to feeding (PF), day of feeding (F1), and day following feeding (F2). Order of diet presentation is given in parentheses.

	Diet				
Fish	A	B	C	D	E
1 PF	133.9	84.5	120.6	118.5	106.0
F1	(2) 208.4	(1) 218.4	(4) 187.5	(3) 189.1	(5) 200.9
F2	168.4	225.9	156.3	163.3	170.7
2 PF	127.1	117.8	151.4	134.9	119.0
F1	(4) 172.3	(3) 186.6	(2) 204.5	(1) 217.1	(5) 186.3
F2	151.7	175.5	210.1	208.6	143.5
3 PF	63.0	119.3	125.7	112.2	112.0
F1	(1) 135.6	(4) 204.5	(5) 206.8	(3) 181.2	(2) 184.1
F2	151.3	190.8	184.5	164.8	132.7
4 PF	107.2	111.5	130.3	127.8	115.4
F1	(4) 157.1	(3) 149.4	(2) 168.9	(5) 164.4	(1) 208.2
F2	130.1	125.8	145.9	149.2	159.8
5 PF	125.9	91.2	112.1	124.9	130.8
F1	(5) 216.5	(1) 188.5	(4) 232.4	(2) 231.6	(3) 244.8
F2	153.9	151.2	181.7	202.0	201.0
6 PF	76.9	103.1	95.3	77.6	64.6
F1	(3) 123.4	(2) 153.0	(5) 150.4	(1) 137.4	(4) 138.2
F2	87.4	101.9	109.8	136.4	122.1

TABLE 4. Percentage of ingested food calories expended for food utilization in six bluegill fed experimental diets at 25 C. A mean value is given for each diet ($\bar{x}j$) and each fish ($\bar{x}i$). $\bar{x}_G \pm SE$ = grand mean ± standard error of the mean.

Fish	Diet					
no.	A	B	C	D	E	$\bar{x}_i$
1	13.2	32.3	12.4	13.1	17.4	17.6
2	10.2	18.3	15.7	21.3	12.2	15.5
3	19.5	18.8	16.6	18.0	10.4	16.7
4	12.0	8.5	8.8	9.1	21.6	12.0
5	12.9	14.0	16.8	16.4	19.8	16.0
6	8.0	7.5	9.6	15.9	16.9	11.6
$\bar{x}_j$	12.6	16.6	13.3	15.6	16.1	$\bar{x}_G \pm SE$ = 14.90±0.96

for each fish and each diet. Values ranged from 7.5 to 32.3% of ingested food energy, with $\bar{x}$ = 14.90 ± 0.96% SE. Analysis of variance indicated no significant differences among the mean responses to varying protein level in the diet.

Significant statistical relationships between protein and caloric intakes and the increases in O_2 consumption after feeding were established through linear regression analysis. More variability was accounted for in the model relating O_2 consumption to caloric intake ($r^2 = 0.623$ for caloric intake; $r^2 = 0.461$ for protein intake). The relationship between caloric intakes and the increases in the rate of O_2 consumption is shown in Fig. 2. Higher statistical correlations were obtained when metabolic responses for the entire 48-h period were used in the regression analyses rather than the data from F1 or F2 days alone. No significant relationship was found between protein or caloric intakes and the estimates of the energy cost of food utilization.

The use of "dummy" variable multiple re-

TABLE 5. Summary of the "dummy" variable multiple regression analysis of the independent variables of protein intake (milligrams per gram body weight) and caloric intake (calories per gram body weight) and the dependent variable of increase in O_2 consumption after feeding (milligrams O_2 per kilogram-hour). *Significant at $P \leq 0.05$; **Significant at $P \leq 0.01$; ANOVA = analysis of variance; NS = not significant.

A. Protein Intake
ANOVA table

Source	df	Mean square	F	
Regression	5	1777	9.53	0.002**
Error	23	208		
Total	28			

Regression model

Source (diet)	df	Regression coef	Partial F
Dummy 1[a] (D)	1	37.81	9.00**
Dummy 2 (C)	1	33.64	8.01**
Dummy 3 (B)	1	22.73	5.00*
Dummy 4 (A)	1	8.18	0.78 (NS)
Protein intake	1	15.12	36.36**

B. Caloric Intake
ANOVA table

Source	df	Mean square	F	
Regression	5	1858	9.75	0.0001**
Error	23	190		
Total	28			

Regression model

Source (diet)	df	Regression coef	Partial F
Dummy 1 (D)	1	−12.97	2.61 (NS)
Dummy 2 (C)	1	−11.29	1.81 (NS)
Dummy 3 (B)	1	−12.16	2.33 (NS)
Dummy 4 (A)	1	−13.81	3.00 (NS)
Caloric intake	1	1.25	41.87**

[a]Based on diet E.

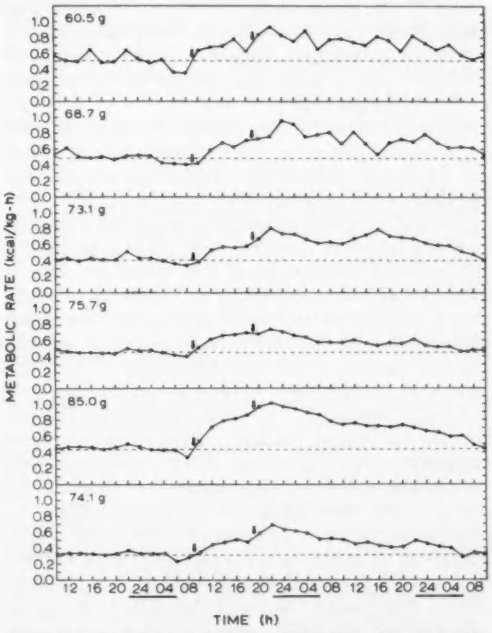

FIG. 1. Average sequential metabolic rates ($n = 5$) of the six experimental fish during prefeeding days (PF), days of feeding (F1), and days subsequent to feeding (F2). Arrows indicate times of feeding. Dark periods on the time scale are underlined. Dashed lines show the average PF rates and serve as references for the increased rates subsequent to feeding.

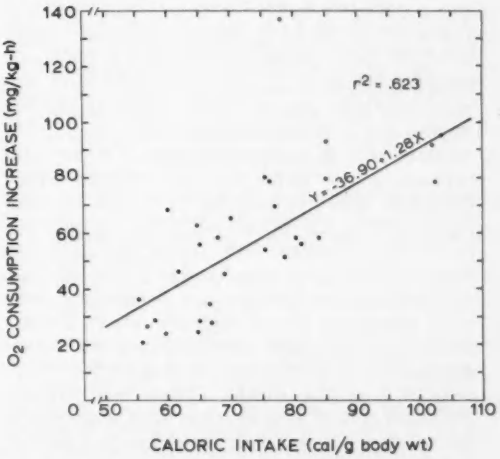

FIG. 2. Relationship of caloric intake and the average increase in rate of O_2 consumption during the 48-h period subsequent to feeding. The value (○) for fish 1, diet B was confirmed as a statistical outlier.

gression analysis improved the regression models for the relationships between protein and caloric intakes and the increases in O_2 consumption after feeding. A summary of the results of these analyses is presented in Table 5. Coefficients of determination (r^2) for the multiple regression models employing caloric intake and protein intake were 0.679 and 0.650, respectively.

Discussion

In this study, food intakes, as percentages of wet body weight, were similar to those reported by Pierce and Wissing (1974) for bluegill fed ad lib. on mayfly nymphs. However, the high organic and low water content of the dry pellet diets resulted in caloric intakes that were 4–5 times higher than those recorded for the natural food item. These differences in ration size and composition may explain differences in the SDA response observed in the two studies. Pierce and Wissing (1974) demonstrated an average increase of 37.7% in the metabolic rate during the day of feeding; these elevated rates generally approached prefeeding levels by the end of the F1 day. Their results contrast with the more pronounced metabolic increases (57%) of longer duration in this study.

Specific dynamic action (SDA) is regarded generally as a postabsorptive phenomenon (Brody 1945), and appears to be highly variable in fish. Saunders (1963) demonstrated that in groups of Atlantic cod (*Gadus morhua*) fed large meals of herring, O_2 consumption remained elevated above starvation levels for about 7 days at 10 C and 4–5 days at 15 C. Muir and Niimi (1972) observed that rations of 2.3 and 4.5% body weight resulted in 42- and 60-h periods of elevated metabolic rate in a 44-g aholehole (*Kuhlia sandvicensis*). More recently, Beamish (1974) reported that in largemouth bass (*Micropterus salmoides*) fed meals of lake emerald shiner (*Notropis atherinoides*) the time for O_2 consumption to return to prefeeding levels was positively correlated with ration size and fish weight. In our study, the duration of the increases in metabolic rate subsequent to feeding was most likely influenced by the digestion rate of the dry food. The data imply that dry food pellets are digested more slowly than a natural food item such as a mayfly nymph (Pierce and Wissing 1974). A similar response has been observed in the rainbow trout (*Salmo gairdneri*) (Windell and Norris 1969).

The mean value of 14.90% of ingested energy as the energy cost of food utilization is similar to the values of 12.7, 16–19, and 14.2% reported by Pierce and Wissing (1974), Muir and Niimi (1972), and Beamish (1974), respectively. Other values for fish, derived by difference from energy budget equations, are generally greater in magnitude. Krueger et al. (1968) reported that SDA accounted for 22% of ingested calories in 1–2-g cichlids (*Cichlasoma bimaculatum*) fed on tubificid worms. Kerr (1971) proposed a value of 28.2% for the brook trout (*Salvelinus fontinalis*), based on data compiled from previous studies of food consumption and growth efficiencies. Brocksen et al. (1968) published estimates of SDA in underyearling cutthroat trout (*Salmo clarki*) fed varying rations of housefly larvae and adults. Their values, as percentages of ingested calories, ranged from 13 to 46% ($\bar{x} = 33.8\%$). The discrepancies among these published estimates to a large extent reflect differences in dietary regime and in the nutritional characteristics of the various diets.

The close correspondence between the grand mean value (12.74%) of the energy cost of food utilization for bluegills fed on mayfly nymphs (Pierce and Wissing 1974) and the value (14.90%) observed in the present study may indicate that the natural and artificial foods were being metabolized with the same efficiency. Possibly, however, the pellet diets were digested and assimilated less efficiently than the natural food. Windell et al. (1969) have noted that providing artificial foods with large proportions of digestible organic matter may pose special digestive problems to fish adapted to foods containing about 5–20% digestible organic matter. The pellet diets used in this study contained higher levels of carbohydrates than those found in the natural food items of the bluegill. In general, carbohydrates in fish are not digested as efficiently as fats or proteins (Phillips 1969).

The absence of a significant trend in the metabolic rates and, consequently, the estimates of the energy cost of food utilization with dietary protein level suggests several explanations. The observed variation among individual fish was high and could have obscured real differences among the diets. Interestingly, if the value for fish 1, diet B (32.3%; see Table 4) is ignored, a slight trend of increasing energy expenditure for food utilization with increasing protein level is present in the means of the diet responses. The differences in protein level among the diets may not be large enough to produce significant increases in the estimates of the energy cost of food utilization with increasing dietary protein level. A final consideration, and perhaps a more likely one, is that the SDA or calorigenic effect of protein in fishes is considerably lower than that observed in other vertebrates, and hence cannot be easily measured, even when dietary protein levels are varied. Many vertebrates are either ureotelic or uricotelic, whereas fishes are almost totally ammonotelic. Brody (1945) has suggested that 20% of the SDA of protein arises from the synthesis of urea and that as much as 25% of the SDA of catabolized protein can be attributed to the work of kidney excretion. Solomon and Brafield (1972) concluded that urea never ac-

counted for more than 5% of the total nitrogen excreted by the perch *Perca fluviatilis*. Thus, the grand mean estimate (14.90%) of the energy cost of food utilization computed in this study could reflect a small energy expenditure associated with the metabolism of assimilated amino acids, along with the calorigenic effect of the lipids and carbohydrates present in the experimental diets.

The results of the regression analyses indicate that for the range of food intakes studied a relatively fixed proportion of the ingested energy is expended by the bluegill for food utilization. Beamish (1974) found no significant differences in largemouth bass between the estimates of apparent SDA and meal size or fish weight. These findings may be attributed to the remarkable metabolic and growth plasticity of fish, which can adjust to a large range of temperature and food conditions in nature. Such adjustments may involve a complex interaction of components of resting and active metabolism with the food energy supply and may imply "underlying feedback or homeostatic mechanisms operating on the dynamic energy system" (Paloheimo and Dickie 1966). Our results are an apparent reflection of these stabilizing mechanisms. In this study, increases in caloric intakes of 400–500% over those reported by Pierce and Wissing (1974) resulted in similar energy expenditures for food utilization.

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Changes in Proximate Composition of the Crayfish *Orconectes propinquus* with Size, Sex, and Life Stage

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STEIN, R. A., AND M. L. MURPHY. 1976. Changes in proximate composition of the crayfish *Orconectes propinquus* with size, sex, and life stage. J. Fish. Res. Board Can. 33: 2450–2458.

We estimated percent water, inorganic material, and chitin for the crayfish *Orconectes propinquus*. To properly account for organic materials and mineral salts, we burned samples first at 550 C then at 650 C for estimates of the inorganic fraction. More precise estimates were obtained at 650 C; thus, to account for the conversion of $CaCO_3$ to CaO and CO_2 at 650 C, inorganic estimates were multiplied by an empirically derived factor (1.5) to convert all values to total inorganic material. For chitin, acid decalcification, followed by deproteinization with base and combustion at 650 C, provided best estimates. Proximate composition varied with size, sex, and molt stage. Percent water was inversely related to size for juveniles but was constant with size in adult males (68.4%) and females (67.4%). Percent inorganic material and chitin of dry weight increased with size in juveniles; inorganic continued to increase with size following maturity while percent chitin remained constant. For a carapace length of 25 mm, adult males had significantly more inorganic material (46.2 vs. 38.1%) and chitin (16.3 vs. 14.1%) than adult females. Differences in proximate composition appeared related to secondary sexual characteristics, with males having longer, wider chelae but narrower abdomens than females. Recent molts had more water (84.1%) and less inorganic (19.0%) and chitin (9.1%) than either male or female intermolts. Understanding how these proximates vary with life stage is necessary for adequately describing transfer of energy and biomass between populations.

STEIN, R. A., AND M. L. MURPHY. 1976. Changes in proximate composition of the crayfish *Orconectes propinquus* with size, sex, and life stage. J. Fish. Res. Board Can. 33: 2450–2458.

Nous avons estimé le pourcentage d'eau, de matière inorganique et de chitine dans l'écrevisse *Orconectes propinquus*. Pour une détermination convenable de la matière organique et des sels minéraux, nous avons incinéré les échantillons d'abord à 550 C et ensuite, pour la fraction inorganique, à 650 C. La combustion à 650 C donne des estimations plus précises; c'est pourquoi, afin de tenir compte de la conversion du $CaCO_3$ en CaO et en CO_2 à 650 C, nous avons multiplié les estimés de matière inorganique par un facteur déterminé empiriquement (1.5), de façon à convertir toutes les valeurs en matière inorganique totale. Pour la chitine, la décalcification acidique suivie d'une déprotéinisation basique et combustion à 650 C fournissent les meilleurs estimés. La composition en première approximation varie en fonction de la taille, du sexe et du stade de mue. La teneur en eau est en relation inverse de la taille chez les jeunes, mais demeure constante en fonction de la taille chez les mâles (68.4%) et les femelles (67.4%) adultes. La matière inorganique et la chitine, en pourcentages du poids sec, augmentent en fonction de la taille chez les jeunes; la matière inorganique continue d'augmenter avec la taille une fois la maturité atteinte, alors que le pourcentage de chitine demeure constant. Pour une longueur de carapace de 25 mm, les mâles adultes contiennent nettement plus de matière inorganique (46.2 vs 38.1%) et de chitine (16.3 vs 14.1%) que les femelles adultes. Les différences dans la composition en première approximation semblent liées à des caractères sexuels secondaires, les mâles possédant des pinces plus longues et plus larges, mais un abdomen plus étroit que les femelles. Les individus qui ont mué récemment contiennent plus d'eau (84.1%) et moins de matière inorganique (19.0%) et de chitine (9.1%) que les individus, mâles ou femelles, au stade d'intermue. Il est nécessaire de comprendre comment cette composition en première approximation varie selon le stade biologique si l'on veut décrire adéquatement le transfert d'énergie et de biomasse entre populations.

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PROXIMATE analysis of organisms, involving the determination of percent water, ash, chitin, and digestible organic, forms the basis for measuring transfer of energy and biomass between populations. Values for these proximates are necessary for any study of ecosystem energetics (Golley 1961; Cummins and Wuycheck 1971; Paine 1971) and, in fact, are commonly applied in work with the nutrition and production of economically important animals (Gerking 1952; Windell 1967; Driver et al. 1974). However, few workers have dealt with the systematic variation of proximates within populations. Most literature values are based on analysis of a few specimens with little or no data on variation associated with size, sex, or life stage, all of which may influence proximate composition (Pepper and Hastings 1943; Tsao and Richards 1952; Cummins and Wuycheck 1971; McComish et al. 1974).

Knowledge of systematic variation in proximate composition should lead to more precise estimates of energy and biomass transfer between populations, especially important in studies of the energetics of predator–prey interactions. For example, current theories of optimal foraging have assumed constant percent digestible matter (i.e. percent available for digestion by potential predators) with respect to prey size (Werner 1974). However, differences in proximate composition within prey populations could alter energetic cost to benefit ratios and conceivably influence patterns of selective predation.

In this paper, we describe the distribution of water, inorganic material, and chitin as functions of size, sex, and life stage in an important prey of inshore fishes, the crayfish *Orconectes propinquus*. Because of methodological problems associated with a large $CaCO_3$ fraction (Paine 1964) within the exoskeleton of crayfish, we also develop a standard method for proximate analysis of freshwater decapods.

Materials and Methods

EXPERIMENTAL ANIMALS

Crayfish were collected from Trout Lake, Vilas County, Wisconsin, during September through October 1973. Berried females, young-of-year, and premolt Form I (FI, capable of breeding) males were collected during June and July 1974. Recently molted animals plus exuviae were obtained by holding premolt FI males in shallow tubs until ecdysis was complete; body and exuviae were then treated separately. For each crayfish carapace length (from tip of rostrum to posteriomedian edge of carapace) to the nearest millimeter, sex, and life stage were determined. For intermolts and recent molts, 1-mm size-classes of adults consisted of 10 crayfish (5 per sex); juveniles (<20 mm) within 1-mm size-classes were combined to form at least five groups of 10 animals per sex. All samples were stored at −15 C prior to analysis.

WET AND DRY WEIGHTS

To estimate wet weight, frozen crayfish were thawed, blotted with paper towels, and weighed to the nearest milligram. For dry weight, crayfish were dried for 48 h at 80 C, cooled over anhydrous Na_2SO_4, and reweighed. Dried animals were then homogenized with a Wiley mill (No. 20 seive) and stored at 80 C.

ESTIMATION OF INORGANIC MATERIAL

To determine combustion temperatures necessary for estimating percent inorganic material in crayfish, we ashed 10 samples for 4 h at 50-C intervals from 500 to 925 C. Most precise estimates were obtained at 650 C (F-test, $P < 0.005$, $n = 15$). In these samples no organic matter persisted. Consequently, 200-mg subsamples of dry homogenized crayfish were weighed into crucibles to the nearest 0.1 mg, burned at 650 C in a muffle furnace overnight, cooled over anhydrous Na_2SO_4, and reweighed. Two subsamples per animal were taken to estimate variance.

Even though combustion at 650 C eliminated all organic matter, this technique also converted $CaCO_3$ to CaO; thus, percent inorganic was not accurately estimated. To determine correction factors, we ashed a series of samples for 4 h at 550 C and again at 650 C overnight. Weight loss between ashings was attributed to CO_2 production from: 1) decomposition of $CaCO_3$ and 2) combustion of residual organic matter. Organic matter persisting in samples ashed at 550 C was estimated by dissolving remaining mineral salts with 10% HCl, filtering through glass fiber filters (GF/C), drying for 48 h at 80 C, and reashing at 550 C for 4 h. The combustible portion of the dried residue was recorded as residual organic. Estimates for total inorganic matter were calculated from the percent of oxide ash by a conversion factor:

$$\frac{100}{100 - AR + RO} \quad (1)$$

where AR (ash reduction) = percent reduction in ash weight between 550 and 650 C; and RO (residual organic) = percent residual organic matter of ash (at 550 C).

Between 550 and 650 C ash weight decreased 34.0 ± 1.2% ($\bar{x} \pm$ SD); percent ash reduction (AR) was constant with respect to size, sex, and life stage of crayfish (F-test). Residual organic (RO) was estimated to be 2.1 ± 0.9% for all groups of crayfish (F-test). Equation (1) therefore yielded a correction factor of 1.5 which was applied uniformly across all groups to convert inorganic estimates at 650 C to total inorganic material.

Crayfish inorganic matter consists primarily of $CaCO_3$ (Richards 1951), some of which is chemically bound to organic material (Travis 1960; Hackman 1971). Loss of water of hydration from these inor-

ganic salts during combustion could result in an underestimation of inorganic content (Paine 1964). Paine's estimates were based on chemically purified calcareous spicules of nudibranchs, free of organic matter. By ashing samples at a series of temperatures (500–900 C), wetting the ash with distilled water, and drying for 48 h at 80 C, we could estimate water of hydration as the gain in ash weight following wetting and drying. For our samples, only after burning at 600 C (after $CaCO_3$ began to decompose and residual organic matter began to burn) did the inorganic portion become hydrated. Organic matter, when chemically bound to the $CaCO_3$, apparently prevented hydration. In nonpurified samples, water of hydration was absent, and thus, should not influence our estimates of percent inorganic.

Chitin Estimation

Samples of about 200 mg each were weighed into 125 ml flasks, decalcified with 100 ml of 10% acetic acid for 48 h, then heated to 100 C. Hot solutions were centrifuged and the acidic solution was replaced with 100 ml of 10% NaOH. Samples were then digested for 72 h, boiled until particles became translucent white, and vacuum filtered through GF/C filters with thorough rinses of 10% HCl, 70% ethanol, and distilled water. Residue and filter were then dried 48 h at 80 C and ashed 4 h at 650 C. Loss in weight of the dried residue during combustion was recorded as chitin.

Pepper and Hastings (1943) considered insect chitin to be the ashable fraction of an alkaline insoluble residue. Because this residue in crayfish contains large quantities of inorganic material, percent chitin could be overestimated by this method due to loss of water of hydration from purified inorganic salts and the decomposition of carbonates during combustion. Furthermore, chemical interactions within the alkaline solution used to digest crayfish might result in precipitation of organic carbonates. Using this method of chitin analysis (Horowitz et al. 1957; Bemiller and Whistler 1962; Hornung and Stevenson 1971; Gwinn and Stevenson 1973), we estimated chitin for a size-stratified sample of crayfish (two replicates per sample). Values obtained approximated our earlier estimates obtained with decalcification but variance was significantly higher than acidified samples (F-test, $P < 0.005$). Decalcification followed by deproteinization and combustion thus provides a more precise method for estimating chitin in crayfish.

We further found that, without decalcifying, the variance within samples varied with respect to the molt cycle. Without decalcifying, we got an organic-carbonate precipitate from homogenized intermolt crayfish with associated high variance. However, when recent molts (within 24 h) or exuviae were analyzed separately, precipitation did not occur, and variance was significantly reduced (F-test, $P < 0.005$).

Calcification of the exoskeleton is accompanied by increases in the insoluble protein fraction with a corresponding decrease in the soluble fraction (Travis 1960). Because chitin is intimately associated with these water-insoluble proteins (Kent 1964; Herzog et al. 1975; Neville 1975), extraction of chitin without the use of extreme conditions (higher temperatures and more concentrated solvents) becomes difficult (Tracey 1957). These changes in the cuticle with calcification could explain the high variability within intermolts; the precipitate might be an organic-carbonate complex not present in the same form in recent molts as in intermolt crayfish.

The presence of precipitates in digestive solutions has not been reported previously. The method cited above, except for Hornung and Stevenson (1971) and Gwinn and Stevenson (1973), used just the cuticle of a decapod, perhaps accounting for absence of a precipitate. Gwinn and Stevenson (1973) digested whole crayfish (*Orconectes obscurus*) with 10% NaOH but for a shorter period (18 h). Following 18 h of digestion, our samples still contained some orange color; thus, we felt longer digestion times were warranted. Rudall (1955) suggests that collagen, a stringy protein found in crustacean cuticles, might convert to a glue or gelatin upon prolonged heating with water. Consequently, these longer digestion periods, which induce collagen to gell, could account for our precipitate.

Mineral deposition in an organic matrix associated with chitin (Kent 1964) makes accurate determination of chitin difficult. Following alkali treatment, chitin becomes a powerful absorbent of organic and inorganic materials (Kent 1964) as well as water (Hackman 1971); removal of mineral salts (primarily $CaCO_3$) prior to deproteinization should reduce the error associated with chitin estimation. Even with prior acidification, however, protein can become bound to chitin during treatment; removal of all protein associated with chitin appears nearly impossible (Foster and Weber 1960; Kent 1964). However, Herzog et al. (1975) found that gentle decalcification with acetic acid, followed by treatment with 1 N NaOH removed all protein from the chitin–protein complex. Thus, our method of chitin estimation probably provides reasonable estimates of percent chitin.

Fecal Analysis

Some fishes are able to utilize chitin (Micha et al. 1973; Colin 1972) while others are not (Kitchell and Windell 1970; Kionka and Windell 1972). If inorganic material and chitin are not assimilated, then absolute amounts of each should not change as they pass through the digestive system of a predatory fish. Thus, to determine if our measure of dry digestible organic material (100% − [%inorganic + % chitin]) accurately reflects the amount of energy available to the next trophic level, we analyzed feces of smallmouth bass (*Micropterus dolomieui*) fed crayfish. Three bass (20–25 cm, total length) in flow-through aquaria at 25 C were fed crayfish (<16 mm) ad lib. for $\simeq$ 15 days. Feces were collected twice each day, dried, stored at 80 C, and analyzed for total inorganic matter and chitin as described above.

TABLE 1. Formulas and statistics relating proximates (Y) to carapace length (x) in crayfish (*Orconectes propinquus*) from Trout Lake, Wisconsin. Figure designations shown in parentheses; NSG = not shown graphically.

Proximates (Y)	Life stage	Carapace length (*mm*) (x)	No. of samples (n)	Regression coef (b)	Y Intercept (a) or $\bar{x} \pm$ SD	Sample SD of regression coef (s_b)
Wet weight	Young-of-year*	4–7	20	2.36	7.13×10^{-4}	0.62
$Y = ax^b$	Juveniles	8–20	220	3.32	1.12×10^{-4}	0.17
(NSG)	Females	19–42	160	2.92	3.56×10^{-4}	0.07
	Berried females	20–32	102	2.95	3.67×10^{-4}	0.09
	FI males	19–38	200	3.01	3.16×10^{-4}	0.31
Dry weight	Young-of-year*	4–7	20	2.10	2.24×10^{-4}	0.45
$Y = ax^b$	Juveniles	8–20	220	3.29	2.13×10^{-5}	0.15
(NSG)	Females	19–34	160	2.67	9.45×10^{-5}	0.18
	Berried females	20–32	102	2.93	1.13×10^{-4}	0.14
	FI males	17–34	200	2.89	1.25×10^{-4}	0.07
% water	Juveniles	4–19	250	−0.41	78.5	0.05
$Y = a + bx$	Females	20–38	249	—	67.4 ± 1.9	—
(Fig. 1a)	Berried females	20–32	102	—	71.3 ± 1.5	—
	FI males	19–38	197	—	68.4 ± 1.7	—
% inorganic	Juveniles	4–21	150	0.26	35.1	0.04
$Y = a + bx$	Females	22–41	60	0.19	33.3	0.05
(Fig. 1b)	Berried females	20–27	102	0.22	34.4	0.06
	FI males	19–38	100	0.20	41.2	0.03
% chitin	Juveniles	4–20	38	0.27	8.6	0.09
$Y = a + bx$	Females	23–36	24	—	14.1 ± 1.7	—
(Fig. 1c)	Berried females	20–27	8	—	14.4 ± 1.2	—
	FI males	23–42	34	—	16.3 ± 1.4	—

*Except for wet and dry weights, young-of-year (4–7 mm) were not significantly different from other juveniles.

DATA ANALYSIS

We plotted wet and dry weight, estimates for percent water, total inorganic, and chitin against carapace length. Throughout, percent water refers to water as a percent of wet weight, whereas percent inorganic and chitin are calculated as percents of dry weight. When no significant differences were found among sex or life stage, data were combined for regression analysis. Generally, data were divided into four groups: juveniles (males and females <20 mm, carapace length), adult females, berried females, and adult males (FI). Mean values in the text are reported as $\bar{x} \pm 1$ SD.

Results

WET WEIGHT

Crayfish wet weight was a power function of carapace length (Table 1); log wet weight was a linear function of log carapace length. Significant regressions were obtained for two groups of juveniles (<8 mm and 8–20 mm) as well as for adults (FI males and females combined). Slopes of regression lines were significantly different for these three groups (F-test, $P < 0.005$). For a given size, berried females were similar in wet weight to adult females. Males weighed slightly less than females prior to 20 mm, but more than females after 20 mm. However, these differences were not significant (F-test).

DRY WEIGHT

Log dry weight was a linear function of log carapace length (Table 1). As before, significant regressions were obtained for both groups of juveniles (<8 mm and 8–20 mm) as well as for adults (females and FI males combined). Slopes of regression lines were significantly different for these three groups (F-test, $P < 0.005$) but similar for both sexes. For a given size, berried females were similar in dry weight to adult females. Weights of FI males and adult females were similar with no difference between means within any size-class.

PERCENT WATER

Percent water was a linear function of carapace length (Fig. 1). Juveniles showed a significant negative slope (t-test, $P < 0.001$); percent water decreased 0.4%/mm. For adults percent water was constant with respect to size at 67.4 ±

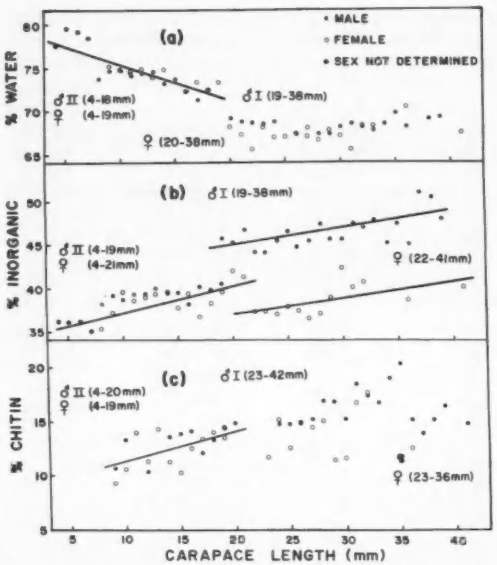

FIG. 1. Mean values (within each 1-mm size-class) for a, percent water, b, inorganic content, and c, chitin, plotted against carapace length for *Orconectes propinquus* from Trout Lake, Wisconsin. Because percent water is given as a percent of wet weight whereas inorganic matter and chitin are given as percents of dry weight, values do not sum to 100%. Lines were drawn only through data with statistically significant slopes. See Table 1 for appropriate regression equations.

1.9%, 71.3 ± 1.5%, and 68.4 ± 1.7% for females, berried females, and FI males, respectively, with no difference among means.

PERCENT INORGANIC

Percent inorganic content was a linear function of carapace length (Fig. 1). Significant regressions (t-test, $P < 0.001$) were obtained for juveniles, adult females, and FI males; berried females were not different from the other females. Among groups, slopes of regression lines were not different (F-test). Percent inorganic for all groups increased approximately 0.2%/mm. Intercepts, however, differed significantly among the three groups (F-test, $P < 0.001$); FI males had highest concentrations of inorganic (44–51%) relative to juveniles and adult females (33–41%).

PERCENT CHITIN

Percent chitin was a linear function of carapace length (Fig. 1). Juveniles showed a significant positive regression (t-test, $P < 0.05$) as chitin increased 0.3%/mm. Percent chitin was constant with respect to size in adults, significantly higher for FI males than females at 16.3 ± 1.4% and 14.1 ± 1.7%, respectively (t-test, $P < 0.05$). Berried and nonberried females had similar percentages of chitin.

FECAL ANALYSIS

Feces from bass fed crayfish contained 66.9% inorganic matter and 22.6% chitin, values similar to those for exuviae of recent molts (Table 2). Similarity between these values suggests that bass are not able to digest inorganic materials or chitin from the exoskeleton of crayfish.

PROXIMATE COMPOSITION (CHANGES WITH SIZE, SEX, AND MOLT STAGE)

Percent inorganic and chitin of dry weight increased with crayfish size; consequently, percent dry digestible (i.e. percent available for digestion by smallmouth bass) decreased (Table 2). Adult females had a larger percent dry digestible than FI males; no differences between males and females were apparent for juveniles. Newly molted FII males (20–34 mm) were 19.0 ± 3.5% inorganic matter ($n = 51$); most inorganic material was probably contributed by gastroliths which develop prior to ecdysis. Percent chitin of dry weight was 9.1 ± 0.5%. Hence, percent dry digestible was 71.9% dry weight (Table 2). Exuviae consisted of 64.5 ± 0.5% inorganic and 25.1 ± 1.6% chitin, values similar to those for feces of fish fed crayfish (Table 2).

Exuviae of FI males made up 50% of their total intermolt dry weight. From this proportion and percentages of various proximates such as inorganic and chitin for body and exuviae immediately after a molt, we estimated the percentages of these proximates retained by crayfish through a molt. When FI males molted to FII, only 25% of their mineral salts and chitin was retained; the great portion of these materials was lost through the molt.

Discussion

WET AND DRY WEIGHTS

Three significantly different regressions were obtained for wet and dry weight vs. carapace length. Differences in length–weight regressions probably reflect changes in either the length–volume function or body composition, i.e. different rates of integumentary calcification or accumulation of fat. Differences between adults and juveniles may be due to allometry of chelae, changes in body shape to accommodate gonads,

TABLE 2. Proximate composition of intermolt and recently molted crayfish (*O. propinquus*). Proximate composition of the feces of smallmouth bass (*Micropterus dolomieui*) fed crayfish are included to permit comparisons with the proximate composition of the exuviae of recent molts. Except for fecal material, values are calculated from formulas given in Table 1.

Life stage	Category	Carapace length (*mm*)	% water		% inorganic		% chitin		% Digestible of dry wt[a]	
			♂	♀	♂	♀	♂	♀	♂	♀
Young-of-year	Whole body	5	76.4		36.4		10.0		53.6	
Juveniles		15	72.3		39.0		12.7		48.3	
Adults		25	68.4	67.4	46.2	38.1	16.3	14.1	37.5	47.8
Adults		35	68.4	67.4	48.2	40.0	16.3	14.1	35.5	45.9
Recent Molts	Body	20–34	84.1	—	19.0	—	9.1	—	71.9	—
	Exuviae	20–34	71.9	—	63.8	—	25.1	—	11.1	—
Juveniles	Feces of fish fed crayfish[b]	<16	—		66.9±1.4 (n = 5)		22.6±2.8 (n = 30)		10.5	

[a]Percent dry weight of crayfish available for digestion by bass, estimated by subtracting percent inorganic plus percent chitin from 100%.

[b]Values are $\bar{x} \pm$ SD with sample sizes in parentheses.

or differences in body composition. Young-of-year differ from larger juveniles perhaps because they were collected during summer. In summer, a season of rapid growth, more water and less inorganic would be expected (Richards 1951).

PROXIMATE COMPOSITION AND CRAYFISH SIZE

Percent water was negatively correlated with size for juvenile *O. propinquus*. Decreases in percent water correspond with increases in percent inorganic and chitin of dry weight. Apparently, addition of dense material to the integument reduces the contribution of water to total weight. Surface area to volume considerations predict that if inorganic and chitin increase with size, then the cuticle should also be increasing in thickness. Consequently, the integument of crayfish, as in other crustaceans (Kent 1964), increases in thickness with size.

Differences in inorganic and chitin, greater in FI males than adult females, may be explained by the strong sexual dimorphism apparent in *O. propinquus*. FI males have longer, wider chelae but thinner carapaces and abdomens than adult females (Stein et al. 1976). Chelipeds contribute nearly 50% of the total dry weight in large FI males but only 35% in females (Stein 1976). Thus, chelipeds should contribute proportionally more inorganic than organic matter (comparisons with the body suggest chelae have 1.2 times as much inorganic material), whereas a wider abdomen or carapace contributes more organic material. Thus, dimorphism in secondary sexual characteristics probably accounts for differences in percent inorganic and chitin between male and female crayfish. No differences in these proximates between sexes for juveniles lends credence to this hypothesis.

The size- and sex-related differences in percent inorganic become important when ecologists present data as calories per gram ash-free dry weight or milliliters O_2 consumed per gram ash-free dry weight. Changes in percent inorganic, which modify ash-free dry weight of individuals, can explain previously observed anomalies in studies of ecological energetics (Paine 1964). Moshiri et al. (1971) found that volume of oxygen utilized by crayfish (*Pacifastacus leniusculus*) was linearly correlated with carapace length. However, following conversion of their values to milliliters O_2 consumed per gram ash-free dry weight, mature animals (50 mm, total length ≡ 25 mm, carapace length) showed a much greater than expected (given the above linear relation between oxygen use and carapace length) oxygen utilization rate compared to immature animals (30 mm, total length ≡ 15 mm, carapace length). Moshiri et al. (1971) suggest that mature crayfish could 1) be more active, 2) exhibit a size-specific response to the lack of substrate in their respiratory vessels, or 3) exhibit differences in percent inorganic. In fact, an increase in inorganic content at maturity (as demonstrated here for *O. propinquus*) could account for these differences. If the percent ash was simply a mean for all sizes, then adjustment for differences in percent inorganic would serve to lower O_2 consumed per gram ash-free dry weight for mature individuals (inorganic: 46%) while increasing it for immature individuals (inorganic: 39%). This adjustment would serve to bring these two values closer to the expected linear relation between O_2 consumption and size,

thereby eliminating the anomaly in O_2 consumption per gram ash-free dry weight between immature and mature crayfish. This example points out the importance of completing accurate inorganic determinations on a sample of individuals from various life stages.

Proximate Analysis and Energetics

Neither chitin nor inorganic materials are available for digestion by bluegill (*Lepomis macrochirus*) (Gerking 1952; Windell 1967; Kitchell and Windell 1970) or rainbow trout (*Salmo gairdneri*) (Kionka and Windell 1972). The similarity in our values for chitin and inorganic between crayfish exoskeleton and fecal material from smallmouth bass fed crayfish also supports this conclusion for smallmouth bass. Consequently, to adequately assess nutritional value of prey organisms to their predators, proportions of inorganic and chitin should be subtracted from total dry weight. The remainder, percent dry digestible, should provide a more realistic measure of nutritional value of prey (Kitchell and Windell 1970).

As crayfish increase in size, the percent dry digestible matter decreases. Larger crayfish are less desirable prey, not only because they are difficult to capture and consume (Stein 1975), but also because they possess less energy per gram than smaller animals. Care must be exercised when developing tests of optimal foraging among size-classes of a prey species; differences in organic matter among various sizes, sexes, and life stages could significantly alter theoretical predictions. In our case, recent molts appear to be the most desirable life stage for consumption by fish predators, both in terms of digestible organic per gram and ease of capture (Stein 1975); differences among intermolt animals are slight and may not affect general conclusions regarding foraging strategies. However, other prey organisms may not lend themselves to such an intuitive analysis. Small differences in proportion organic (<10%) could lead to a strong bias for one prey organism (e.g. Stein et al. 1975).

Furthermore, digestion rates of fishes may depend on cuticle composition of their prey. Alewives (*Alosa pseudoharengus*) digest *Daphnia* more rapidly than other planktonic crustaceans; therefore, *Daphnia* are often underrepresented in stomach contents, resulting in relatively low estimates of selectivity for this prey item (Gannon 1976). Gannon (1976) goes on to suggest that cuticle composition is probably species specific. As we have shown here, even life stages within one species have unique cuticular compositions. Thus, cuticular composition, by influencing digestion rate and representation in stomachs, may affect measures of predator selectivity.

Consequently, studies of selective predation should take into account variability in 1) percent dry digestible matter and 2) digestion rate between as well as within species of prey. With each new prey item, proximate analysis of a few animals across several size-classes should serve to evaluate those factors that could influence predator selectivity.

Calcium Conservation

Crayfish are "good hyperosmotic regulators" and show active uptake of ions from dilute media (Prosser 1973). Because maintenance of ion concentrations against diffusion gradients requires energy, mechanisms for conservation of calcium during ecdysis would be expected. Calcium concentration has been shown to limit survival and distribution of *O. propinquus* (Capelli 1975). Thus, 25% retention of inorganic matter through a molt (primarily by storage in gastroliths) seems low. If conservation of calcium is important to survival of *O. propinquus*, shouldn't larger amounts be retained? At 10.5 mg/liter, calcium is probably not limiting in Trout Lake; in environments with less calcium, would greater amounts be retained through ecdysis? Accordingly, synthesis of chitin requires biochemical energy; why eliminate 75% of this important cuticular polysaccharide with each molt? Other cuticle components, such as lipids, are digested from the cuticle prior to ecdysis and thus are conserved (Richards 1951). One way crayfish might conserve cuticular components is through consumption of exuviae. We have observed *O. propinquus* feeding on exuviae in nature. In support of this observation, Capelli (1975) found large proportions of cuticular particles in the guts of *O. propinquus* collected from Trout Lake. In laboratory aquaria, molting crayfish usually consume nearly all of their exuviae in 48 h. To what extent chitin and inorganic complexes might be assimilated during this process is unknown.

Conclusions

Understanding how proportions of digestible organic vary with size, sex, and life stage of prey organisms is necessary for adequately describing interactions between predator and prey. For reliable estimates of inorganic content, prey organisms with large $CaCO_3$ fractions must be ashed first at 550 C and then at 650 C to properly account for organic material and mineral salts. Chitin must be estimated using techniques that call for prior acidification to eliminate interfer-

ence from organic carbonates during deproteinization with NaOH. Finally, with each prey organism, proximate analysis of a few animals across various size, sex, and life stages serves to eliminate this variable as a factor that might confuse interpretations of predator–prey interactions.

Acknowledgments

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Ecology of Arctic Populations of Lake Trout, *Salvelinus namaycush*, Lake Whitefish, *Coregonus clupeaformis*, Arctic Char, *S. alpinus*, and Associated Species in Unexploited Lakes of the Canadian Northwest Territories

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JOHNSON, L. 1976. Ecology of arctic populations of lake trout, *Salvelinus namaycush*, lake whitefish, *Coregonus clupeaformis*, Arctic char, *S. alpinus*, and associated species in unexploited lakes of the Canadian Northwest Territories. J. Fish. Res. Board Can. 33: 2459–2488.

The available data on the fish populations of 35 lakes in the Northwest Territories are examined. The lakes range in size from Great Bear Lake (31, 156 km²) to Keyhole Lake (46 ha); they are situated between lat. 60 and 75° N, east from the Mackenzie River to the west coast of Hudson Bay. Lake trout (*Salvelinus namaycush*) and whitefish (*Coregonus clupeaformis*) form the main populations of the mainland lakes and together make up to 95% of the total catch. There is a trend toward increasing importance of whitefish with decreasing severity of conditions. Most populations show a uni, bi-, or trimodal length distribution; age distributions are unimodal. No change in these distributions was observed over a large number of years in certain lakes. These populations are considered to have reached a climax condition comparable with a vegetational climax, and are therefore in equilibrium with their environment. All incoming energy is ultimately used in respiration to support a high biomass of fish.

JOHNSON, L. 1976. Ecology of arctic populations of lake trout, *Salvelinus namaycush*, lake whitefish, *Coregonus clupeaformis*, Arctic char, *S. alpinus*, and associated species in unexploited lakes of the Canadian Northwest Territories. J. Fish. Res. Board Can. 33: 2459–2488.

L'auteur analyse les données disponibles sur les populations de poissons de 35 lacs des Territoires du Nord-Ouest. La superficie de ces lacs varie de celle du Grand lac de l'Ours (31 156 km²) à celle du lac Keyhole (46 ha); ils sont situés entre les latitudes 60 et 75° N, et depuis l'est du fleuve Mackenzie jusqu'à la côte occidentale de la baie d'Hudson. Les populations de touladis (*Salvelinus namaycush*) et de grands corégones (*Coregonus clupeaformis*) prédominent dans les lacs de la terre ferme et constituent, à elles deux, jusqu'à 95% des prises totales. On observe une tendance à l'augmentation chez le grand corégone à mesure que les conditions deviennent moins sévères. La plupart des populations montrent une distribution bimodale ou trimodale des longueurs; la distribution des âges est unimodale. Dans certains lacs, il n'y a pas eu de changements dans ces distributions pendant plusieurs années. On considère ces populations comme ayant atteint un climax comparable à une végétation au stade climatique et étant donc en équilibre avec leur environnement. Tout l'apport d'énergie est utilisé en dernier lieu dans la respiration servant au maintien d'une biomasse élevée de poissons.

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THE Canadian Northwest Territories is one of the few remaining regions in the world where a large number of lakes exist unmodified by man's agency. These lakes are comparatively young having developed in isolation since the retreat of the last Pleistocene glaciation, 8,000–12,000 yr ago.

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The lakes in this arctic region vary enormously in size, from Great Bear and Great Slave lakes at over 30,000 km², through a vast number of intermediate size down to the myriads of small tundra lakes and ponds.

The winter climate common to all lakes is severe in intensity and duration; this is followed by a short summer which, at least on the mainland, is comparatively warm. In winter between 1 and 3 m of ice develop on the surface of the

lakes and it is the rate of melting of this ice which greatly influences summer conditions; the interaction between climate and morphology of the individual lake gives rise to great differences in the internal environment. Great Bear Lake (66°N) retains its ice until the second half of July, nearly 6 wk after Keller Lake (64°N) becomes ice-free. Keller Lake may reach an isothermal condition at 13 C soon after the point of maximum heat intake in August (L. Johnson unpublished data), whereas Great Bear Lake circulates close to 4 C throughout most of the short summer (Johnson 1975a). In this respect Char Lake (75°N) is comparable with Great Bear Lake: it becomes ice-free slightly later than Great Bear Lake, circulating at 4 C when heat intake reaches a maximum (Schindler et al. 1974). Char Lake freezes in early September and Keller Lake in October, but Great Bear Lake is not completely ice-covered until the beginning of December. These lakes are among the more extreme in their response to climate; the majority of the lakes to be considered are intermediate in their regimes.

Except for the smallest ponds all the lakes in the region support fish populations; however, the fauna of any given lake is determined, not only by the opportunities for migration that have been available to each species (McPhail and Lindsey 1970), but also by the environment within that lake (Johnson 1975b).

Although primary productivity in arctic lakes is low (Kalff 1970; Kalff and Welch 1974) it is evidently sufficient to maintain relatively simple food webs leading to high standing crops of fish; the individual fish in these populations are, characteristically, of large size. As a result, the large standing crops of large fish have popularly given rise to the impression that these waters have considerable potential for exploitation; it is equally apparent that the low primary productivity is inadequate to support a high rate of harvest in the terminal parts of the food web.

Over the last 30 yr investigations, primarily directed at the assessment of fish stocks and their potential rates of exploitation, have yielded considerable information on northern lakes. It is the purpose of this paper to examine this material and to attempt some generalizations on the ecological processes involved, generalizations that in all probability can only be developed through consideration of unmodified systems.

Materials and Methods

The material for this paper was collected over a number of years by many people. In 1945 Miller and Kennedy (Miller 1947; Miller and Kennedy 1948; Kennedy 1949) carried out the first fishery surveys in northern Canadian lakes. Grainger (1953) started a study on Arctic char (*Salvelinus alpinus*) in the Sylvia Grinnell River and Frobisher Bay, Baffin Island, in 1948 that continued for 3 yr. This was followed by several years of intensive work by the Arctic Unit of the Fisheries Research Board (now the Arctic Biological Station of the Fisheries and Marine Service, Department of the Environment): in 1959 a survey of lakes in the barren grounds, that area of mainland Canada north of the tree line and west of Hudson Bay, was carried out by J. G. Hunter; Johnson (1964, 1972, 1973) investigated lakes in the arctic archipelago and northern mainland; and Johnson (1975a, b, c) carried out a study of Great Bear Lake between 1963 and 1965. A detailed study of Arctic char production in "Keyhole" Lake was made by Hunter (1970) between 1963 and 1967. In 1967, the Canadian section of the International Biological Programme established a research station at Char Lake, Cornwallis Island (Bigler 1972) which operated until 1973. In 1967 surveys of Nonacho and Kakisa lakes were carried out under my supervision. A survey of Lac la Martre was undertaken by Bond (1973) in 1972 in connection with a commercial fishery established there. Fiona Lake, Somerset Island, was reexamined by de March and Eddy (1976) in 1975. Monitoring of the sportfishing on Great Bear Lake was conducted by the Operations Directorate of the Fisheries and Marine Service (Falk et al. 1974). Test fishing results obtained by the Operations Directorate have been of much value.

More recently in 1973 a new study was initiated by the Freshwater Institute (Research Directorate, Fisheries and Marine Service, Department of the Environment) on the production of anadromous Arctic char at "Nauyuk" Lake on the Kent Peninsula, Northwest Territories. This program, under my supervision, embraces subsidiary studies on landlocked populations in "Little Nauyuk," "Gaviafaeces," and "Klondike" lakes and included return visits to Keyhole and Namaycush lakes in 1975.

With few exceptions the early collections of fish were made with standard gangs of nylon gillnets of graded mesh size. The standard gang consisted of the following mesh sizes (stretched measure): 1½ in. (38 mm), 2½ in. (62 mm), 3½ in. (89 mm), 4½ in. (114 mm), and 5½ in. (140 mm). These nets were set as a single gang wherever possible but were divided into two or more sets where this was not practical. In Great Bear Lake in 1964 and 1965 only 3½-, 4½-, and 5½-in. mesh nets were used as the smaller sizes had been almost completely unsuccessful in 1963; in Keyhole Lake the largest mesh used was 3½ in. and the smallest ¾ in., owing to the small size of the fish present. The nets used in test fishing were exclusively 4½- and 5½-in. mesh, the only legal sizes in the Northwest Territories.

In 1974 and 1975 two new experimental gillnets were introduced with great success, particularly for smaller fish; one net consisted of six panels, each 20 m long and 1.8 m deep, each panel being of a different mesh size (stretched measure): 20, 38, 66,

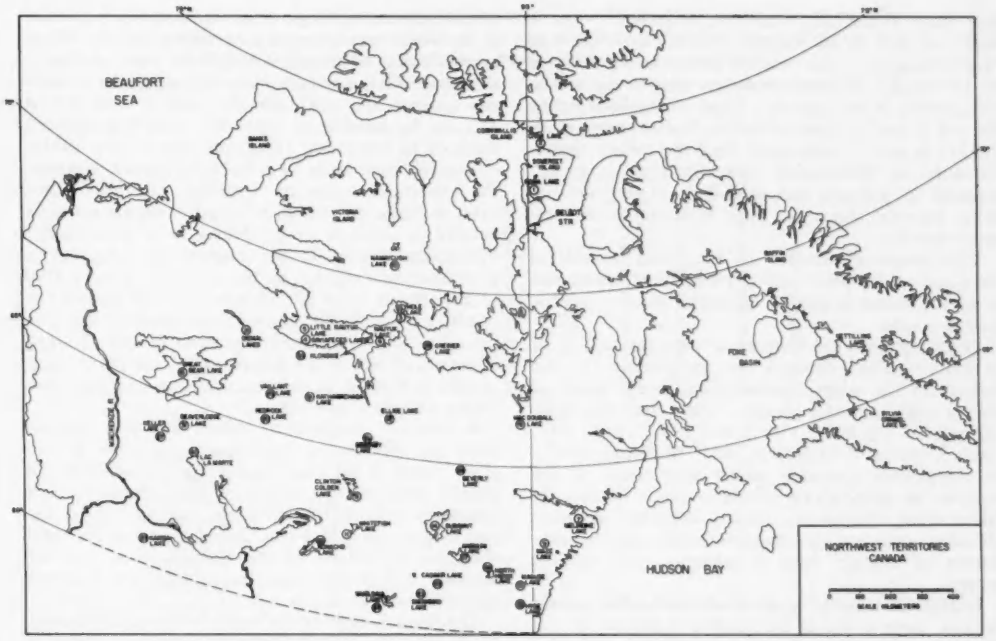

FIG. 1. Northwest Territories of Canada with the locations of the lakes referred to in the text.

90, 110, and 120 mm stretched measure. The second net was similar but with the following mesh sizes: 20, 25, 32, 38, 44, and 50 mm. The nets used prior to 1973 will be referred to as standard gangs and the two newer gillnets will be called experimental nets when fished simultaneously.

To supplement the experimental nets electrofishing has been used on an increasing scale owing to the recent development of functional battery operated equipment.

Some samples were occasionally taken using fish poison, notably the 1962 sample of Arctic char from Fiona Lake, Somerset Island. In Char Lake rod and line and fine-meshed trap net were both used extensively.

The most unbiased sample, and perhaps the most extensive, was taken at the Nauyuk Lake counting fence which was operated on both upstream and downstream migrations in 1974 and 1975. The information on this system was supplemented by use of experimental gillnets, trapnets, seines, and electrofishing gear.

Immediately after capture the fork length was measured in millimeters and the fish was weighed as accurately as possible, to the nearest gram for fish under 50 g, to the nearest 10 g for fish 50–1,000 g, and to the nearest 25 g for fish in excess of 1,000 g.

Scales from the region immediately below the posterior edge of the dorsal fin were taken for aging whitefish (*Coregonus clupeaformis*), lake trout (*S. namaycush*), and walleye (*Stizostedion vitreum vitreum*); the sagittal otolith was removed for aging lake trout and char.

Fish in northern waters are notably slow growing (Miller and Kennedy 1948; Grainger 1953; Johnson 1973; Falk et al. 1974) so that aging presents some difficulty. This is particularly so with fish over 25 yr of age. Good agreement was obtained between various samples taken in Great Bear Lake over a considerable number of years. Miller and Kennedy (1948) used scales, I used scales and otoliths, and Falk et al. used only otoliths. For fish up to 20–25 yr of age agreement was good between scales and otoliths, but in older fish otoliths tend to give higher values: these are probably closer to the truth. Johnston (1975b) obtained two tag returns from lake trout that had been at liberty for 8 and 9 yr respectively, following tagging; these fish were 627 and 953 mm at tagging and 635 and 959 mm on recapture. The small amount of growth, particularly by the larger fish, casts doubt on whether annuli are laid down in the otolith when there is essentially no growth in length. The possibility therefore exists that the age of very slow growing fish may be underestimated.

The lakes with which this paper is concerned are all north of the Northwest Territories boundary (60°N) and lie between the Mackenzie River in the west and Hudson Bay in the east. The most northerly example is Char Lake (75°N) on Cornwallis Island close to the present position of the North Magnetic Pole. Within this large study area the lakes vary in

size from Great Bear Lake (31,152 km²) and a depth of 445 m to Keyhole Lake (48.6 ha) and "Little Nauyuk" Lake (46 ha) with maximum depths of 16 and 6.5 m, respectively. In trophic status they all probably have a primary productivity level below the 100 $g \cdot cm^{-2} \cdot y^{-1}$ established by Vollenweider et al. (1974) as an arbitrary upper limit for carbon assimilation in an oligotrophic lake. However, large differences in primary and secondary productivity do occur between lakes, but these have yet to be measured directly.

The names of several of the lakes considered have not yet received official recognition; where this is so the name is put in quotation marks the first time it is used.

Great progress has been made over the last 25 yr in plant ecology through the examination of the differences in plant communities along lines of known environmental change, rather than the study of units of vegetation (Whittaker 1951, 1953, 1965, 1967; Curtis and McIntosh 1951; McIntosh 1967). A comparable approach seems appropriate to the analysis of populations across a large number of lakes where the species remain relatively constant although experiencing changing environmental conditions of climate, lake morphology, and nutrient supply.

Briefly the concept of gradients states that species existing along a line of environmental change do not have sharp boundaries at points which might correspond to well-defined physiological limits of tolerance. Each species appears to have a central mode or peak of maximum density which decreases gradually on either side; the curves appear to be binomial or Gaussian in form (Whittaker 1967; Brown and Curtis 1952).

As each species responds differently to the environmental variables vegetation is conceived as being primarily "a complex continuum of populations rather than a mosaic of discontinuous units" (Whittaker 1967). A plant community is a particular limited area in which there is no marked progressive change toward a different kind of vegetation, and the sum of the environmental factors, or as Billings (1952) prefers the gestalt of interrelated factors, that affect the community is its environmental complex.

The analysis of vegetation directed toward elucidating the effect of environmental variables, including that of associated species, is termed gradient analysis. This may be direct gradient analysis in which species are arranged and studied according to known magnitudes (or indices of position) along an environmental gradient that is the accepted basis of the study, or indirect gradient analysis in which the axis may or may not correspond to environmental gradients; but if they do correspond, the approach to these environmental gradients is indirect or inferential (Whittaker 1967).

The first stage in the analysis of fish populations of northern lakes is based on the principles of indirect gradient analysis. The methods, in this context, are still in their formative state and before further progress can be made data must be collected with this specific purpose in mind. The same is true of direct gradient analysis; here, it is as yet uncertain as to which environmental variables, against which species could be arranged, might be most profitably measured. Only through trial will satisfactory methods emerge and until specific data is collected it will not be possible to apply the more sophisticated methods of ordination (Whittaker and Gauch 1973).

Use has been made of a further botanical concept, the importance value of a species. The importance value is "some expression of massiveness, conspicuous activity or interest of a species in a community" (Whittaker 1967). If the importance value for a given species is divided by the total of the same kind of importance value for all species in the sample the resulting value is the relative importance value. For fish species in a community the most readily obtained importance value is the percentage by weight of each species in a series of catches taken by one gear type within a single community.

Satisfactory importance values for fish communities are difficult to determine as controls on the effectiveness of the gear; the representativeness of the sample and the boundaries of the community are extremely difficult to determine except through the sampling process. However the adequacy of the sampling can be judged by the frequency and type of anomaly that occurs when the samples are analyzed on the basis of gradients.

The second stage of the analysis is an examination of the structure of individual populations within a community and the development of equilibrium within that community.

Results

General Trends

The general distribution of northern freshwater fishes has been given by McPhail and Lindsey (1970) much of whose material was obtained from the same collections as are discussed in this paper.

North of Viscount Melville Sound, Bellot Strait, and Davis Strait, the only fish species encountered is Arctic char (*Salvelinus alpinus*) with the exception of the two sticklebacks *Pungitius pungitius* and *Gasterosteus aculeatus* which occur in southern Baffin Island. Arctic char exist throughout lakes in the northern islands, either as anadromous populations making short feeding trips to the sea in summer, or, where uplift of the land has isolated the lakes from the sea, as landlocked populations. Migratory and nonmigratory char populations often exist together in the same water body; both types are known to be present at the northernmost limit of land in Lake Hazen (83°N), Ellesmere Island (Anon. 1959).

To the south of Viscount Melville Sound, lakes in Victoria Island have a more varied fish fauna; six additional species are encountered: lake trout (*S. namaycush*), lake whitefish (*C. clupeaformis*)

TABLE 1. Lakes supporting populations of Arctic char (*Salvelinus alpinus*) lake trout, (*S. namaycush*), and associated species of fish and macroinvertebrates in waters close to the Arctic Ocean. Figures in parentheses indicate associated groups of lakes.

		Species present									
Lake	Elevation (*m*)	*S. alpinus*	*S. namaycush*	*Coregonus autumnalis*	*C. sardinella*	*Myoxocephalus quadricornis*	*Gammarus lacustris*	*Gammaracanthus loricatus*	*Mesidothea entomon*	*Mysis relicta*
Fiona	150	X								
Char	30	X								
Keyhole (2)	30	X								
Gaviafaeces (1)	65	X								
Little Nauyuk (1)	30	X							X	X
Namaycush (2)	100		X	X	X					X
Klondike (1)	10		X		X	X	X			
Nauyuk (1)	10	X	X	X	X	X	X	X	X	X
Greiner (2)	26	X	X	X	X		X	X	X	X

and subsequently referred to in this paper simply as "whitefish," least cisco (*C. sardinella*), Arctic cisco (*C. autumnalis*), the fourhorn sculpin (*Myoxocephalus quadricornis*), and the ninespine stickleback (*P. pungitius*). Crossing to the northern mainland, lakes are found that contain in addition to the foregoing; burbot (*Lota lota*), northern pike (*Esox lucius*), round whitefish (*Prosopium cylindraceum*), broad whitefish (*C. nasus*), longnose sucker (*Catostomus catostomus*), and Arctic grayling (*Thymallus arcticus*); however, distribution is unpredictable for any given situation. Away from the coastline lake cisco (*Coregonus artedii*) replaces Arctic and least ciscos in lakes but not in major rivers.

In the drainage basin of Great Bear Lake and lakes further south three more species are added to the list: pickerel or walleye (*Stizostedion vitreum vitreum*), lake chub (*Couesius plumbeus*), and trout-perch (*Percopsis omiscomaycus*). In the Great Slave Lake basin the list increases considerably but the only additional species mentioned in this paper is the white sucker (*Catostomus commersoni*) which forms a considerable fraction of the total fish population in Kakisa Lake.

In the islands and along the mainland coast, species composition appears to be influenced by competitive exclusion particularly in lakes where there is no access to the sea. The number of fish species is reduced as is also the number of macroinvertebrate species considered to be marine-glacial relicts (Johnson 1962, 1964). Where there is access to the sea, char, lake trout, two species of cisco, and whitefish all exist together (Greiner, Nauyuk lakes) as well as the relict species: *Mysis relicta* (Mysidacea), *Mesidothea entomon* (Isopoda), and *Gammaracanthus loricatus* var. *aestuariorum* (Amphipoda); the freshwater amphipod *Gammarus lacustris* is sometimes present. Where the lake is isolated from the sea, either char or lake trout alone is present; usually, it is char which survive and appear to eliminate many of the invertebrate species in addition to the trout (Table 1). Where lake trout survive rather than char, at least one species of cisco is also found (Klondike and Namaycush lakes). Nauyuk, Little Nauyuk, Gaviafaeces, and Klondike lakes are all adjacent and it may be assumed that they all derived their faunas from the same species pool. Nauyuk Lake, which is the most recent to emerge from the sea, has eight species of fish present and three marine-glacial relict macroinvertebrates; the number of species declines with isolation from the sea until only char remain in Gaviafaeces Lake. A similar series exists between Greiner and Keyhole lakes in Victoria Island.

GRADIENTS

The great majority of lakes on the mainland have populations in which lake trout and white-

TABLE 2. Lakes of the Northwest Territories showing relative importance value of species present and the ratio of lake whitefish (*C. clupeaformis*) to lake trout (*S. namaycush*). Lakes with Arctic char (*S. alpinus*) indicated (X) but their relative contribution to the species cannot be calculated (for full explanation see text).

Lake	*S. alpinus*	*S. namaycush*	*C. clupeaformis*	*C. nasus*	*C. artedii*	*C. sardinella*	*C. autumnalis*	*Prosopium cylindraceum*	*Thymallus arcticus*	*Esox lucius*	*Catostomus commersoni*	*C. catostomus*	*Lota lota*	*Stizostedion vitreum*[a]	*Coregonus clupeaformis*: *Salvelinus namaycush*
Klondike		73.50				26.50									—
Meliadine	X	99.5					0.5								—
Maze	X	91.9					3.6	3.8	0.3				0.5		—
Clinton-Colden		89.32			2.93			3.17	4.56						—
Ellice		90.09	7.8					0.89	1.21						0.09
Whitefish		79.65	5.31		4.32			7.47	0.49			2.72			0.06
Namaycush		89.97	9.21			1.27	8.67								0.11
Kathawachaga	X	77.37	9.16				8.83	3.22	1.29						0.12
Nauyuk	X	54.39	8.1			7.5	29.9								0.15
Dubawnt		78.52	15.03		0.05			2.03	0.86			3.39	0.11		0.19
Angikuni 1958		70.21	17.01		1.03			9.62	0.40			1.54			0.24
Great Bear 1964		78.85	18.77							2.30		0.01		0.01	0.24
Maguse	X	56.61	13.59		3.51			4.48		0.35		21.44		20.01	0.24
Beechey		77.59	19.46					1.58	0.60			0.53	0.31		0.25
Great Bear 1963		75.32	20.71		0.69			0.80		2.41		0.06		0.01	0.27
Great Bear 1965		68.40	24.13		0.04			0.01	0.01	6.10		0.34		0.50	0.35
Redrock		63.87	33.93	0.34				1.17		0.46					0.53
Angikuni 1968		63.92	35.96						0.11						0.56
Casmir		60.32	34.75							4.92					0.58
Snowbird		58.02	35.55							6.43					0.61
Wholdaia		44.81	27.62							27.33	0.05	0.17			0.62
Dismal		51.84	34.36	5.05		0.49	8.34	0.42	0.11						0.66
Nonacho		53.26	41.82		0.01			0.03		3.98	0.13	0.63	0.12		0.79
MacDougall		50.83	42.07					3.81	2.80						0.83
North Henik		48.89	51.11												1.05
Keller		40.66	51.46					2.60	20.01	6.83		0.02	0.01	0.72	1.27
Beverly		39.99	51.45		0.34			0.56	0.11	7.44		0.09			1.29
Beaverlodge		31.41	49.85		20.01			20.01		18.66					1.59
Vaillant		35.47	59.68					0.48	2.03	1.48		20.01	0.79		1.68
La Martre 1972		29.17	60.19		20.01							10.64			2.06
La Martre 1959		29.25	63.51		20.01			0.96		5.54		0.71			2.17
Hyde		4.61	54.04		0.11			0.03		40.57		0.51	0.11		11.72
Kakisa 1946[b]			27.92		0.01					5.85	25.38	0.89		39.95	—
Kakisa 1968			14.09		0.01					24.32	21.61	1.26		38.71	—
Winnipeg[c]			69.46	—	0.2	—	—			1.3	0.67	—	—	27.43	—

[a]Combined total of walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*) is given under *S. vitreum*. Not included is 0.94% of other species, mostly yellow perch (*Perca flavescens*), freshwater drum (*Aplodinotus grunniens*), etc.
[b]Data from Kennedy (1946).
[c]Data from Annual Report, Manitoba Department of Mines, Resources and Environmental Management (1972).

fish predominate (Table 2). Such lakes range from those in which lake trout are present without whitefish (e.g. Clinton-Colden Lake) through those in which both species coexist in approximately equal proportions (e.g. Snowbird, Wholdaia, Nonacho, and Keller lakes) to those in which whitefish are the most abundant (e.g. Beaverlodge and Hyde lakes).

Certain lakes are known in the more southerly part of the region in which walleye assume the greatest importance value (Kakisa Lake, also Lac Ste. Thérèse and others designated as "pickerel lakes" under the Northwest Territories Fishery Regulations, Anon. 1974). These pickerel lakes are turbid and shallow and, although they contain whitefish, they are devoid, in general, of lake trout. These lakes probably do not belong to the main lake trout–whitefish series but form a subseries of their own.

One limit of the lake trout–whitefish series is formed by those lakes which contain only lake trout; the other limit seems to be the large lakes, outside the Northwest Territories boundary, such as Southern Indian Lake (McTavish 1952; Ayles and Koshinsky 1975) or Lake Winnipeg (Hewson 1959, 1960) which are completely devoid of lake trout. The relative importance value of lake trout and whitefish in the lakes that lie between these extremes is plotted in Fig. 2. In the majority of cases the points fall close to the line that indicates that together they make up 95% of the total fish population; there is no clustering of values which might suggest an association of the two species in which constant proportions develop.

Lakes in which species other than lake trout or whitefish form a significant fraction of the population are readily identified by their position away from the 95% line; Hyde, Wholdaia and Beaverlodge lakes have high relative importance

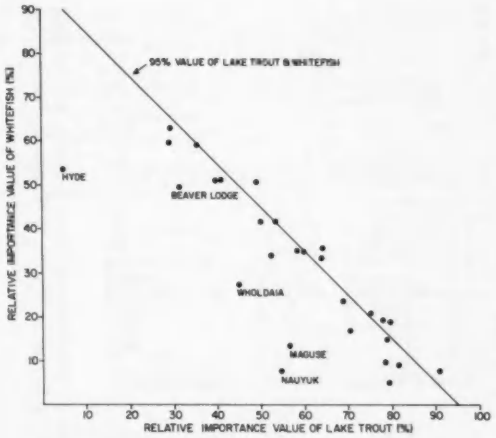

FIG. 2. The relationship between the importance values of lake trout, *Salvelinus namaycush*, and lake whitefish, *Coregonus clupeaformis*. The diagonal line represents the series of values of combined lake trout and whitefish which together equal 95% total catch by weight.

values for northern pike and Maguse is high in longnose suckers. It is not possible to incorporate anadromous Arctic char into such an ordering as the bulk of the population leaves the lake in summer, thus making it impossible to obtain true relative values. Dismal Lake is somewhat anomalous as large numbers of Arctic cisco were taken during sampling, but this high incidence is masked when abundance is considered in terms of importance value.

POPULATION STRUCTURE

By gillnets — The length-frequency distribution of the total catch of the standard gang and that from the individual mesh sizes have been plotted for each lake. A series of histograms was obtained that shows a remarkable degree of uniformity in the size of fish taken by each mesh size in each lake. The grouped results all show well-defined dome- or bell-shaped curves (Fig. 3–6). The modal size for each mesh within a given lake remains remarkably constant within a species, whether it be char, lake trout, or whitefish being considered, but the modal size between lakes for each species varies greatly.

For the experimental nets only total catches are plotted; these all produce bell-shaped curves but over a wide range of modal sizes. The catching ability of these nets at the small end of the scale is demonstrated by the results from Gaviafaeces Lake (Fig. 7), with a modal value between 100 and 120 mm and Little Nauyuk Lake with a well-defined mode at 220 mm (Fig. 7); the char from Keyhole Lake (1975) show a modal value of 314 mm and Lake Namaycush (1975) lake trout, the largest in the series, 693 mm. Little Nauyuk, Keyhole, and Namaycush lakes (Fig. 7) were also fished along the shoreline using electrofishing gear. Keyhole and Namaycush lakes were sampled previously in the early 1960s using a wide variety of gear.

From all the gillnet results the catch curve is either unimodal: Little Nauyuk, Fiona, and Gaviafaeces (char); or bimodal: Keyhole Lake (char), Namaycush Lake (lake trout), Vaillant Lake (whitefish) (Fig. 3), Lac la Martre (whitefish 1972, lake trout 1959, 1972) (Fig. 3), and Kathawachaga Lake (lake trout) (Fig. 4). The remainder shows only a single well-defined mode (Fig. 8 and 9) but the existence of a smaller mode is not precluded as the gear was not sufficiently effective to catch fish of a size below about 250 mm. In populations with a bimodal distribution the second mode may show up either to the right or left of the main peak. A subsidiary mode of very large lake trout can be observed in Lac la Martre in 1959 and 1972; this mode is noticeable in every mesh size. If the second mode is to the left of the main peak it tends to show up only in the smaller mesh sizes (e.g. Nonacho Lake, lake trout and whitefish, Fig. 3 and 4).

The mode varies considerably in the length at which it occurs within a species between lakes (Table 3, Fig. 3–10). Arctic char modes vary from 153 mm in Gaviafaeces Lake and 225 mm in Little Nauyuk Lake to 592 mm in Maguse Lake. Lake trout modes range from 486 mm in Vaillant Lake to 745 and 789 mm in Beaverlodge and Namaycush lakes, respectively. Whitefish are the most uniform species with modes from 426 mm in Beverly Lake to 549 mm in Redrock Lake. The mean size of whitefish in Ellice Lake is 633 mm. In the majority of lakes whitefish peaked at about 500 mm (e.g. Great Bear, Dismal, and Vaillant lakes).

The mean length of fish caught by each mesh size varies more than does the length at which the mode occurs. This seems to result from each mesh having a minimum size of fish which can be retained while showing no evidence for a maximum. This is demonstrated in Table 4 where the 1½-in. mesh captures the greatest size range whereas the 5½-in. mesh catches the smallest range of sizes. The 4½-in. net is the most efficient measured by the number of fish caught; the 1½ in. is the least efficient.

When all lakes, for which there is comparable information, are considered there is a high cor-

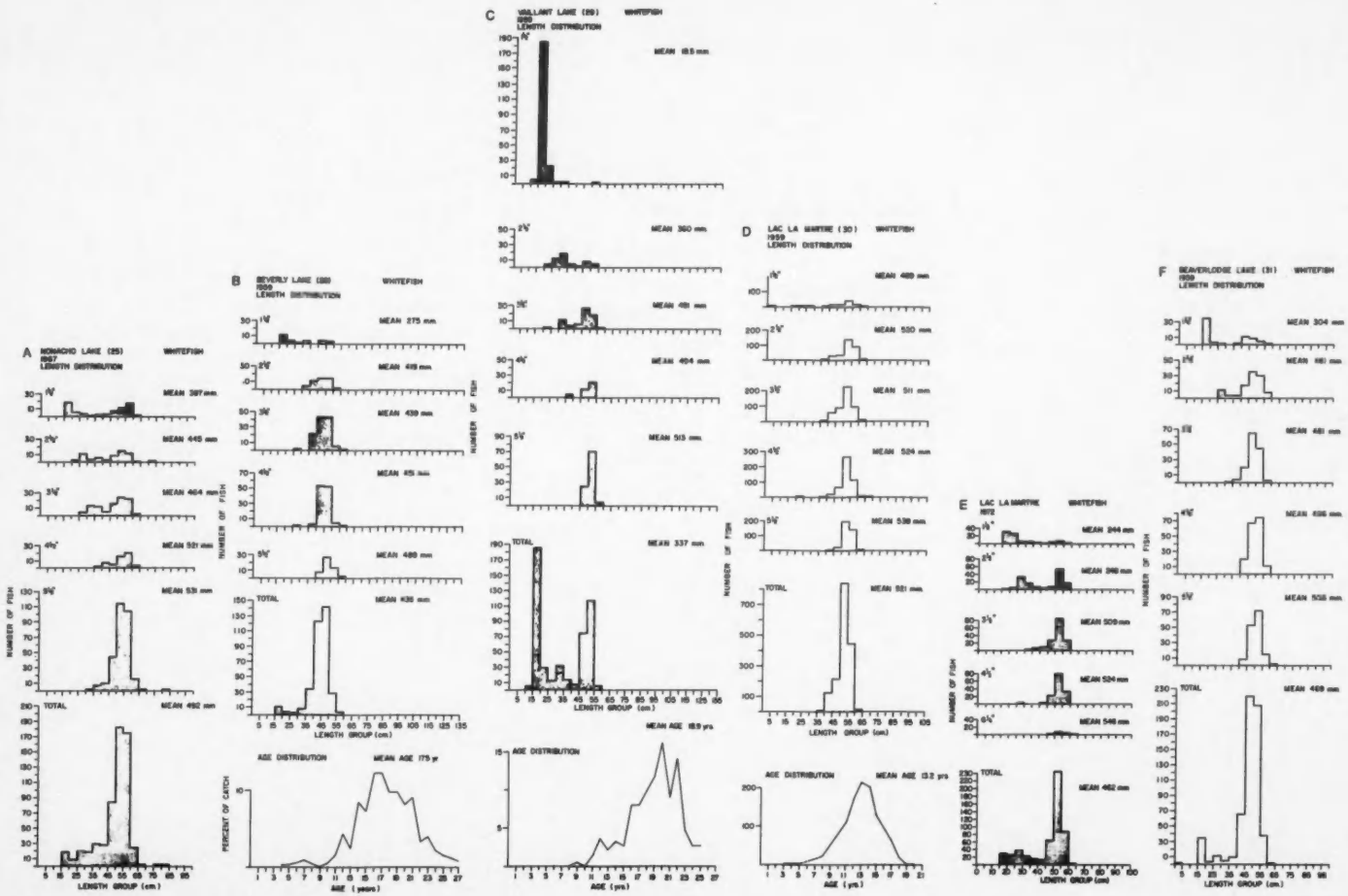

FIG. 3. Length-frequency distributions of lake whitefish, *C. clupeaformis*, by mesh size, with age-frequency distributions where available for the total catch from A, Nonacho Lake 1967; B, Beverly Lake 1959; C, Vaillant Lake 1959; D, Lac la Martre 1959; E, Lac la Martre 1972; and F, Beaverlodge Lake 1959. Data for Lac la Martre 1972 from Bond (1973).

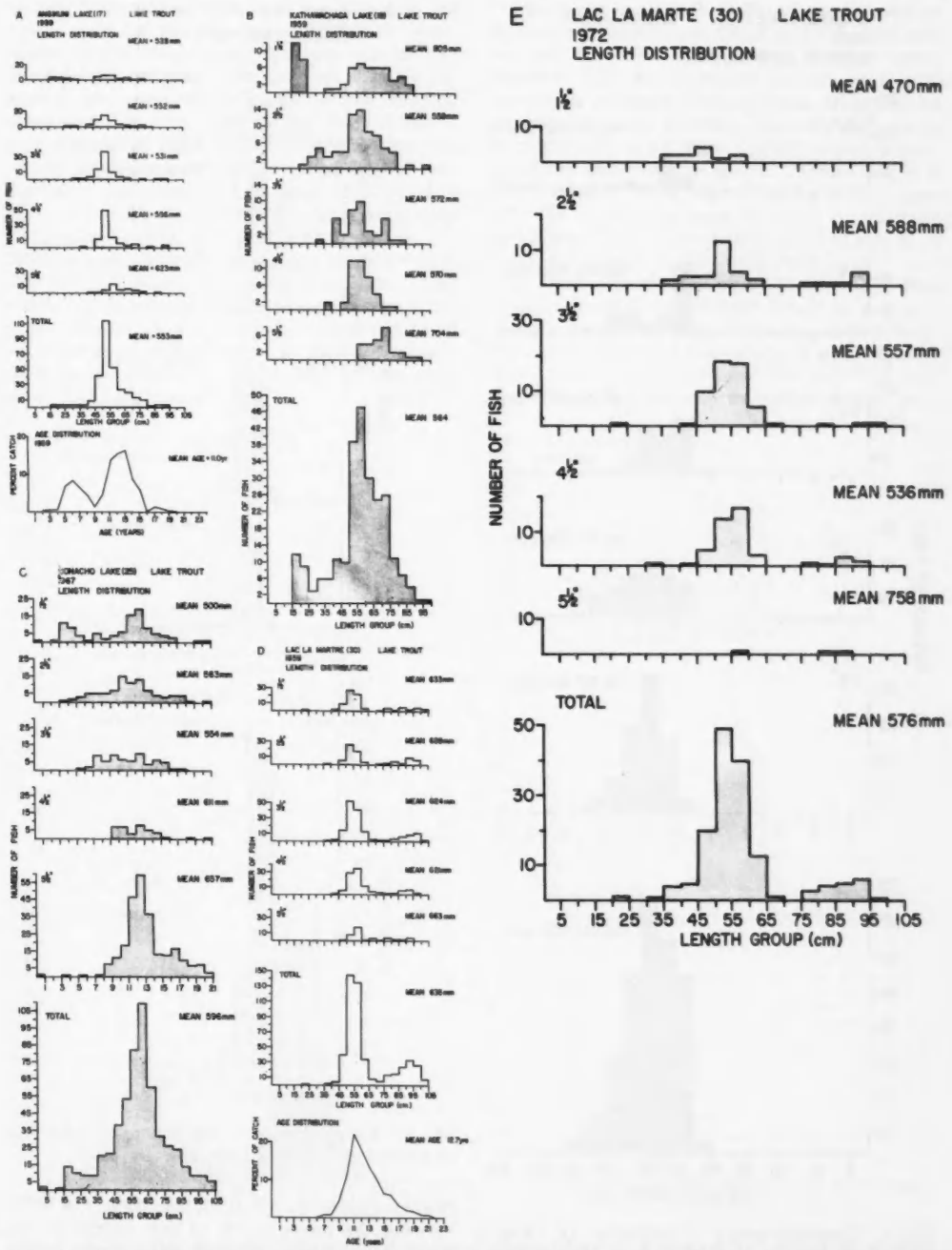

FIG. 4. Length-frequency distributions of lake trout, *S. namaycush*, by mesh size, with age-frequency distributions where available, for total catch from A, Angikuni Lake 1959; B, Kathawachaga Lake 1959; C, Nonacho Lake 1967; D, Lac la Martre 1959; and E, Lac la Martre 1972. Data for Lac la Martre 1972 from Bond (1973).

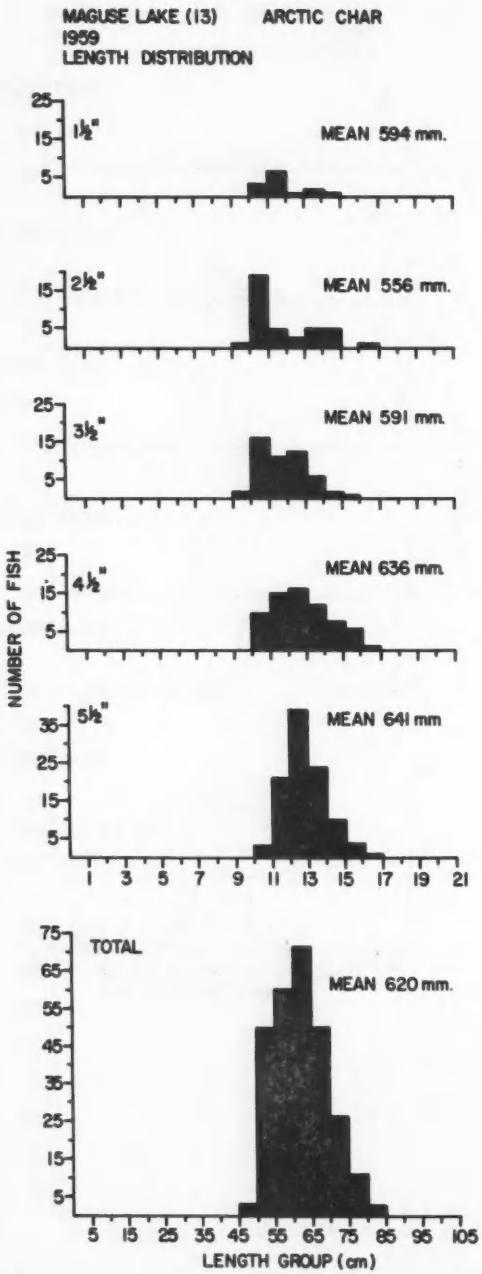

FIG. 5. Length-frequency distribution of Arctic char, *S. alpinus*, by mesh size, from Maguse Lake 1959.

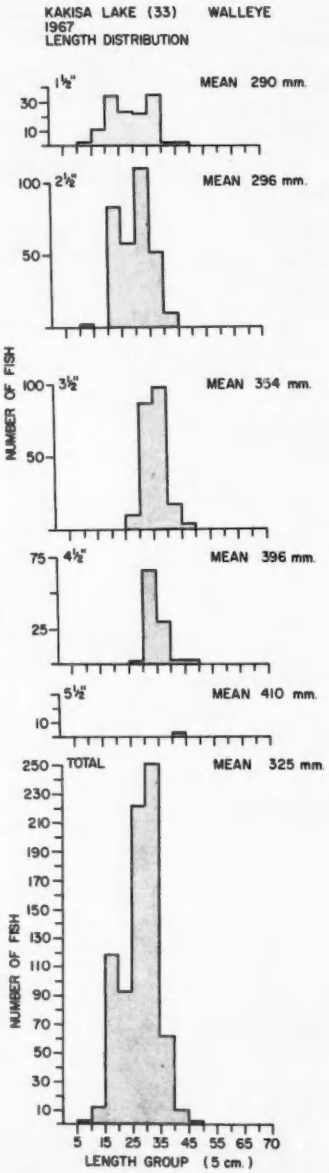

FIG. 6. Length-frequency distribution by mesh size of walleye from Kakisa Lake 1967.

relation (whitefish, $r = 0.94$; lake trout, $r = 0.87$) between the mean length of fish caught by the whole gang and the smallest mean length of fish caught by any individual mesh size (Fig. 10).

Usually the smallest mean size was taken in the 1½-in. mesh but this was not invariably the case. Stated briefly this means that the greater the mean length caught by the gang as a whole the greater the mean length caught in the smallest mesh size. The size taken in any mesh is therefore dependent upon the fish present and not wholly on the capacity of the net to "select" any particular size group. Any detectable selective effect is taking place within a lake; such may sometimes be observed in the slight shift of the mode toward the right as the size increases (e.g. whitefish: Beaverlodge, Nonacho lakes; lake trout: Lac la Martre, Kathawachaga lakes; Arctic char: Maguse Lake). The shift is small compared with the great differences in mesh size and also with the differences in modal size for the same mesh from different lakes.

This is not to deny the effect of mesh selection in certain circumstances (Kipling 1957; McCombie and Fry 1960; Regier and Robson 1966; Hambly 1975) but to negate the conclusion that the results obtained from northern lakes can be attributed to mesh selection. The wide differences in modal size in all three species amply demonstrate the ability of the gear to capture fish in a wide variety of sizes when they are in fact present. The capture of large numbers of whitefish in Vaillant Lake between 150 and 200 mm is of great significance in this connection.

In only a few lakes were species other than char, lake trout, or whitefish taken in sufficient quantity to prepare length-frequency distributions. The northern pike of Beaverlodge Lake (Fig. 11) had a modal value between 700 and 750 mm; apart from this instance the other species were

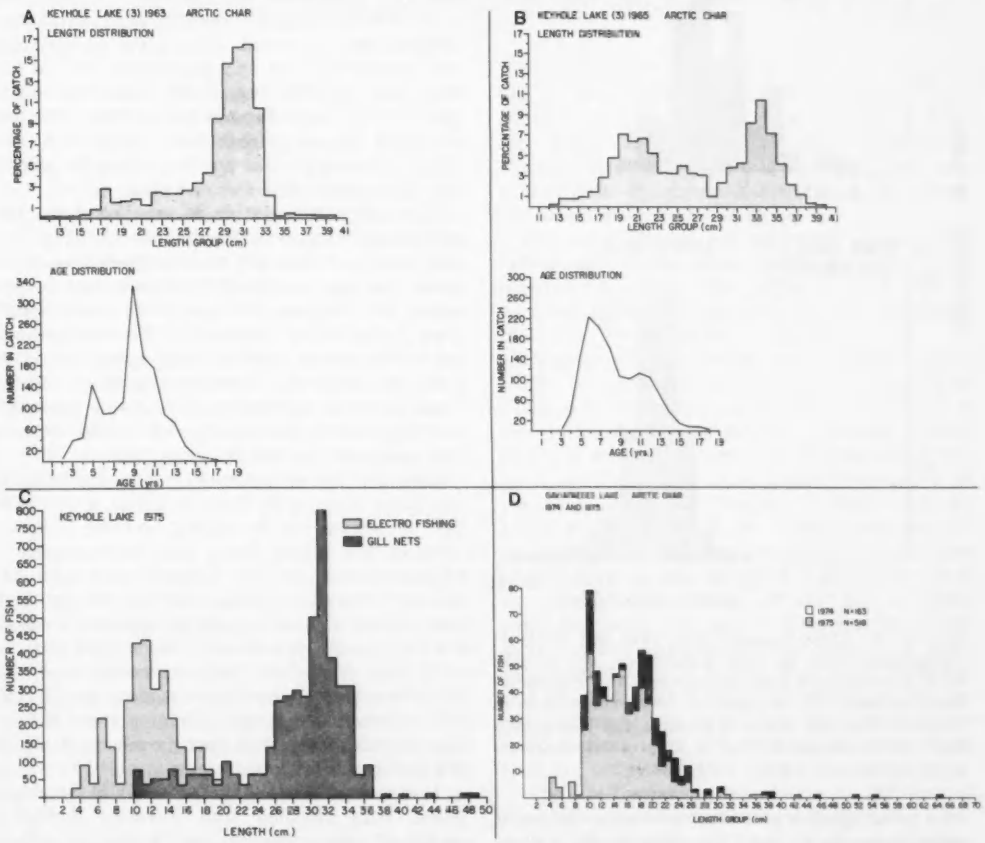

FIG. 7. Length-frequency distribution of Arctic char, *S. alpinus*, from A, Keyhole Lake 1962–63; B, Keyhole Lake 1965; C, Keyhole Lake 1975; D, Gaviafaeces Lake 1974 and 1975;

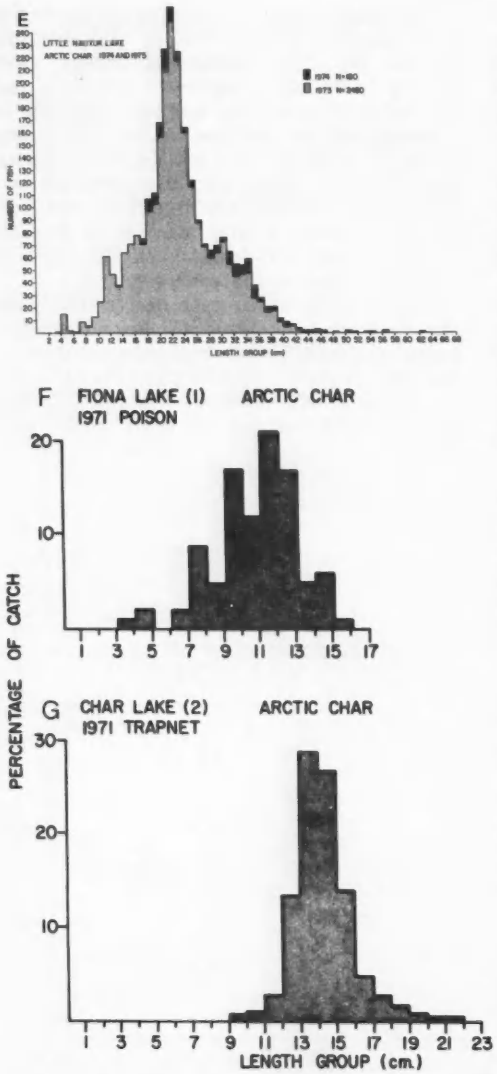

FIG. 7. E, Little Nauyuk Lake 1974 and 1975; F, Fiona Lake 1962; G, Char Lake 1971; and H, lake trout, *S. namaycush*, from Namaycush Lake. Figures for Keyhole Lake 1975 adjusted to the numbers taken in 1962–63. The two modes in Keyhole and Namaycush lakes are not expected to be in the proportions shown as the methods of capture were different.

of a much smaller size compared with the major populations. In Kakisa Lake (Fig. 6) the walleye had a modal size of about 300 mm, the Arctic ciscos of Dismal Lake, 250 mm, and the round whitefish of Whitefish Lake also 250 mm (Fig. 11).

The modal length of walleye from Kakisa Lake in 1967 is considerably smaller than that obtained by Kennedy (1962) in 1946 but the stock has been regularly fished commercially in the interval.

By methods other than gillnets — The Arctic char population of Nauyuk Lake has been sampled more intensively than that of any other northern lake; it probably ranks among the most intensively sampled of any fish population. The sampling was carried out by means of a counting fence established across the river down which the char migrate to the sea. The population has, to date, been observed over 2 yr (1974 and 1975); during this time seaward and return movements have been monitored. The entire seagoing population was counted through the fence during the upstream migrations in 1974 (N = 10,960) and 1975 (N = 10,290) and a high percentage weighed and measured. During the period when the greater part of the population was at sea (late July to early August) the lake was investigated for nonmigrating char; none above 200 mm in length were captured except for certain individuals moving farther up the system for spawning (Campbell and Johnson 1976).

The seaward migrating population shows two well-defined modes at 580 and 200 mm (Fig. 12). The char in the smaller mode migrated when the main run had completed its downstream movement, thus keeping the two groups separate in time (Johnson and Campbell 1975). At least two more size groups exist in fresh water, being too small to make the seaward migration; one of these groups is ephemeral made up of young-of-the-year. The various groups reflect the complex life history of this species.

Over the 2 yr of observation there has been no significant change in the population apart from that accounted for by fishing pressure. Tag returns of 70% show that a very low mortality is experienced in the sea. Growth rates over the summer migration period are exceedingly high particularly in view of sea temperatures below 4 C; a specific growth rate for weight of 1.1–1.5%/day (80–113% weight increase in 45–50 days) has been shown for tagged fish in the 250–300 mm size range, falling to about 0.7%/day for fish above 600 mm; however, much of this increase is lost over winter.

The char in Fiona Lake (Fig. 7) in Somerset Island were sampled with rotenone during a period of intense feeding on chironomid pupae which was taking place along the shoreline. Nets set for a short period in deeper water failed to catch any fish. All the poisoned fish were of a very small size, but one female of 130 mm was

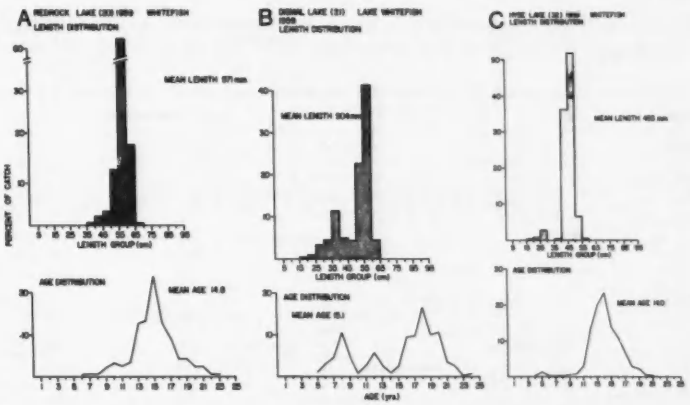

FIG. 8. Length-frequency distribution of lake whitefish, *C. clupeaformis*, all mesh sizes combined, from A, Redrock Lake 1969; B, Dismal Lake 1959; and C, Hyde Lake 1959.

found to contain 24 eggs. The lake was again visited in 1975 by de March and Eddy (1976) who set gillnets and caught several large fish (310–655 mm) but did not capture any small char, as the mesh was not sufficiently fine. The four largest fish were all found to be cannibals.

Char Lake on Cornwallis Island was sampled intensively with rod and line and a small-meshed trapnet (MacCallum 1972) (Fig. 7) as part of the International Biological Programme. A length-frequency distribution, with a well-defined mode at 130–144 mm was derived from the 2,700 char caught in the trapnet; angling yielded essentially the same results. There is an indication that a second mode at a much smaller length was present in that many small fish were observed along the shore (H. Welch personal communication).

Shape of the catch curve for age and length — An emergent character of the catch curves, for age and length, for whitefish and lake trout in Keller Lake was that they show a frequency close to that of a normal distribution curve (Johnson 1972). Many of the catch curves of other arctic lakes have a similar tendency; it is the objective of this section to examine the departure of the curve from the normal or Gaussian condition in terms of being more peaked (leptokurtic) or less peaked (platykurtic) (Croxton and Cowden 1965).

The results (Table 3) show an almost invariable occurrence of the leptokurtic condition in the catch curves for length. This indicates a high degree of clustering around the modal value. In some cases (e.g. whitefish, Redrock Lake, Fig. 8) the condition is extreme with 62% of the population falling in a 50-mm size-class (550–599 mm). Only two lake trout populations (Beaverlodge and MacDougall lakes) are less peaked than in a normal distribution; no whitefish samples were of this type.

The high degree of clustering around the modal value in the curves derived from the combined catches of the five different mesh sizes is of great significance in refuting the contention that the normal-shaped distribution can be ascribed to gillnet selection or to reduced vulnerability in length-groups below that of the modal value. The clustering around the same value is seen in all mesh sizes which, if reduced vulnerability is the reason, would imply that vulnerability is reduced at the same length irrespective of the mesh considered. One size of mesh might be highly selective for fish of a certain narrow size-group, but that five widely different mesh sizes should all be equally selective at the same size is not credible. The ability of the nets to catch small fish (over 250 mm) is shown in the results from Vaillant Lake and Dismal Lake. It is much more satisfactory to believe the results obtained and conclude that the nets are catching a reasonably representative sample of the population, at least in sizes over 250 mm, in the area where they are set.

The age-frequency distribution in the various populations has been examined in the same manner; in the majority of cases a normal or leptokurtic condition exists. The only significantly platykurtic distribution for age was found in the Arctic char from Sylvia Grinnell Lake (1948–51). This age distribution is for the fish actually

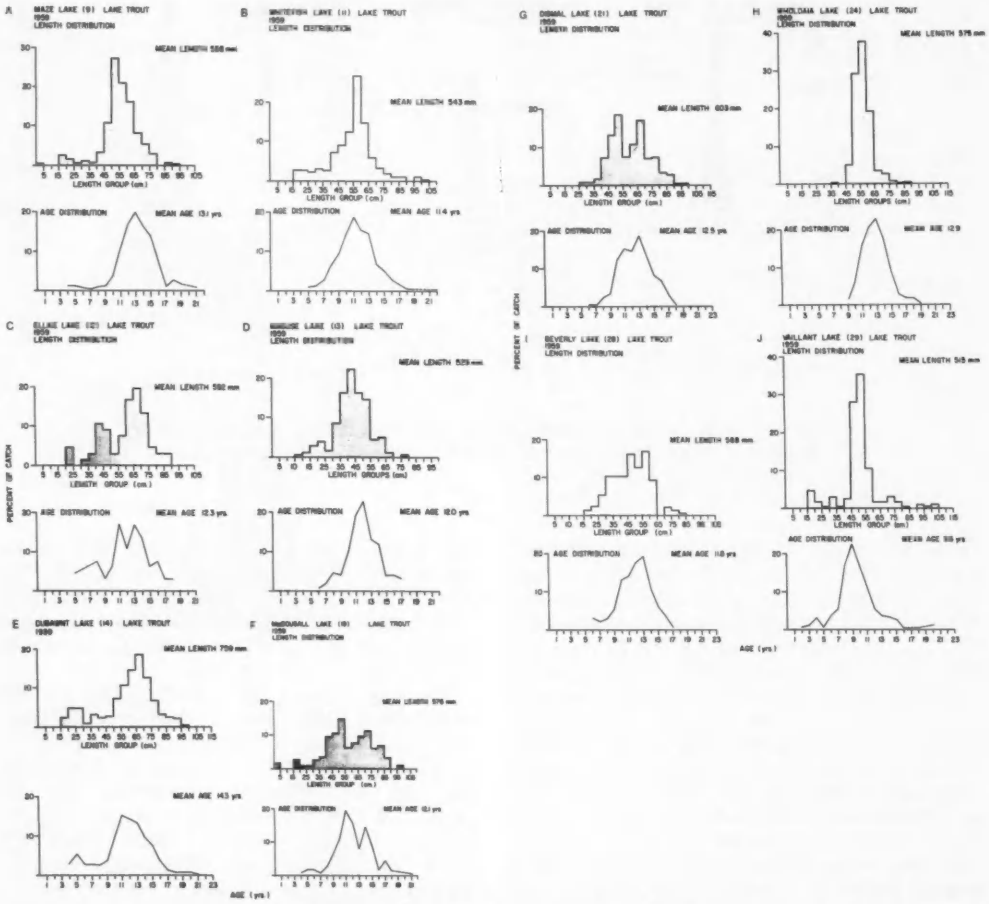

FIG. 9. Length-frequency distribution of lake trout, *S. namaycush*, all mesh sizes combined, from A, Maze Lake 1959; B, Whitefish Lake 1959; C, Ellice Lake 1959; D, Maguse Lake 1959; E, Dubawnt Lake 1959; F, MacDougall Lake 1959; G, Dismal Lake 1959; H, Wholdaia Lake 1959; I, Beverly Lake 1959; J, Vaillant Lake 1959.

caught and states nothing about the age of fish below the limit of vulnerability which is considered to be about 250 mm in the standard gang.

Northern fish populations are of great age (Fig. 3–5, 7–9); the modal age of whitefish lies between 12.7 yr (Lac la Martre, Fig. 9), 17.0 yr (Great Bear Lake, Fig. 13), and 18.9 yr (Vaillant Lake, Fig. 3). The condition in Vaillant Lake is unusual in that there are two pronounced modes at lengths of 215 and 504 mm although only a single mode on the age-frequency distribution.

In lake trout, modal ages range from 11.8 yr (Beverly Lake, Fig. 9) to 18 yr (Great Bear Lake, Fig. 14); a mean age of 31 yr was obtained from Lake Namaycush (1962) although individual ages were so widely distributed as to give no indication of any clustering in spite of a well-defined modal value for length.

Sequential results from the same lake — Several lakes were sampled more than once, often after a lapse of many years. Great Bear Lake experienced three sampling periods over 30 yr, Angikuni Lake was fished in 1959 and 1969, Lac la Martre in 1959 and 1972, and Keller Lake in 1962 and briefly again in 1974. Keyhole Lake was fished heavily in 1962–1967 and revisited in 1975; Lake Namaycush was visited in 1962 and 1975.

TABLE 3. Populations of lake trout (*Salvelinus namaycush*), Arctic char (*S. alpinus*), and lake whitefish (*C. clupeaformis*) from lakes in the Northwest Territories, showing mean and modal length, mean and modal age and departure of population curve from a normal distribution. $*P < 0.005$; $**P < 0.01$.

Lake	Length (*mm*)			Age (*yr*)		
	Mean	Mode	Kurtosis	Mean	Mode	Kurtosis
			S. namaycush			
Maze	557±112	534	Leptokurtic**	13.4±2.11	13.5	Leptokurtic**
Ellice	596±128	667	Normal	—	—	
Namaycush						
(1962)	775±150	855				
(1975)	693±133	765	Leptokurtic**	—	—	
Whitefish	543±149	578	Leptokurtic*	11.4±2.46	11.6	Leptokurtic**
Great Bear						
(1945)	562±136	573	Normal	17.47	17.0	
(1963–65)	639±117	636	Leptokurtic**	18.7±4.14	17.95	
(1973)	664± 99	637	Leptokurtic**	24.75	20.0	
Dubawnt	649±124	621	Normal	12.6±2.39	12.9	Leptokurtic**
Kathawachaga	599±126	566	Normal	15.1±2.40	14.5	Normal
Angikuni (1959)	555±113	527	Leptokurtic**	13.3±2.04	13.1	Leptokurtic
Maguse	519±112	525	Normal	12.0±2.21	12.2	Normal
Nonacho	596±161	618	Leptokurtic*	—	—	
Dismal	601±132	593	Normal	12.5±2.19	11.5	Normal
MacDougall	598±155	517	Platykurtic*	12.1	11.7	Normal
Wholdaia	575± 76	565	Leptokurtic**	12.9±1.82	13.3	Leptokurtic
Keller	579±107	572	Leptokurtic**	16.2±3.84	16.9	Leptokurtic
Berverly	569±130	671	Normal	11.8±2.30	13.6	Normal
Vaillant	512±141	512	Leptokurtic**	9.6±2.34	9.5	Leptokurtic**
Beaverlodge	765±144	875	Platykurtic**	14.3±2.51	14.3	Normal
La Martre						
250–749 mm	550± 53	547	Leptokurtic**	12.7±2.8	11.75	Leptokurtic**
700–999 mm	895± 78	903	Normal			
Hyde	651± 19	649	Normal	14.2	14.3	—
			S. alpinus			
Fiona	107± 23	119	Normal			
Char	148± 17	149	Leptokurtic**			
Keyhole						
(1963)	289± 42	308	Leptokurtic**	8.8±2.74	9.6	Leptokurtic**
(1975)						
30–220 mm	122± 40	111	Normal			
220–480 mm	306± 31	314	Normal			
Gaviafaeces	153± 48	—				
Little Nauyuk	231± 64	226	Normal			
Maguse	621± 73	618	Normal	9.9±1.24	9.2	Leptokurtic**
Nauyuk	583±122	602	Normal			
Sylvia Grinnell						
(1948–51)	526±134	531	Platykurtic	14.41±4.1	13.6	Platykurtic*
(1950)	517±138	612	Normal			
			C. clupeaformis			
Great Bear	515± 69	531	Normal	16.9±3.9	16.8	Normal
Redrock	569± 44	576	Leptokurtic**	14.8±2.7	15.5	Leptokurtic*
Dismal	503± 99	566	Normal			
			(5–14 Yr)	9.9±2.3	8.5	Normal
			(14–24 Yr)	18.3±1.894	18.5	Normal
Wholdaia	422± 63	462	Leptokurtic**	—	—	—
Nonacho	495±105	547	Leptokurtic**	—	—	—
Keller	562± 88	567	Leptokurtic**			
			(2–10 Yr)	5.6±2.24	7.2	Normal
			(11–26 Yr)	18.4±2.50	18.9	Normal
Beverly	446± 48	457	Leptokurtic*	17.3±3.9	17.16	Normal
Vaillant						
100–450 mm	215± 70	176	Leptokurtic**	18.9±3.2	20.4	Normal
400–600 mm	504± 80	514	Normal			
La Martre	522± 48	528	Leptokurtic**	13.2±2.3	13.8	Leptokurtic*
Beaverlodge	492± 45	499	Leptokurtic**	—	—	—
Hyde	453± 49	463	Leptokurtic**	14.2±1.93	14.3	Leptokurtic**

In 1945, Miller (1947) carried out the first survey of Great Bear Lake using cotton nets of 2½-, 3-, 4-, and 5-in. mesh sizes (stretched measure). The lake was sampled again by Johnson in 1963–65 (Johnson 1975b) and by Falk et al. (1974) who in 1973 obtained data from anglers' catch.

The age- and length-frequency distributions of lake trout from these three periods are shown in Fig. 13. There is little change in the distribution with time, for either age or length. Falk used otoliths exclusively for aging; these seem to give slightly higher readings up to 20 yr and considerably higher ages in older fish.

The change over the same period in the size of whitefish in Great Bear Lake is negligible (Fig. 14). This species is harvested by the native Indian domestic fishery in restricted areas so that the figures are for an essentially unexploited population.

Lac la Martre was sampled in 1959 during the survey of the barren grounds and again by Bond (1973) in 1972. Between 1969 and the start of the fishing season in 1972, it was estimated that

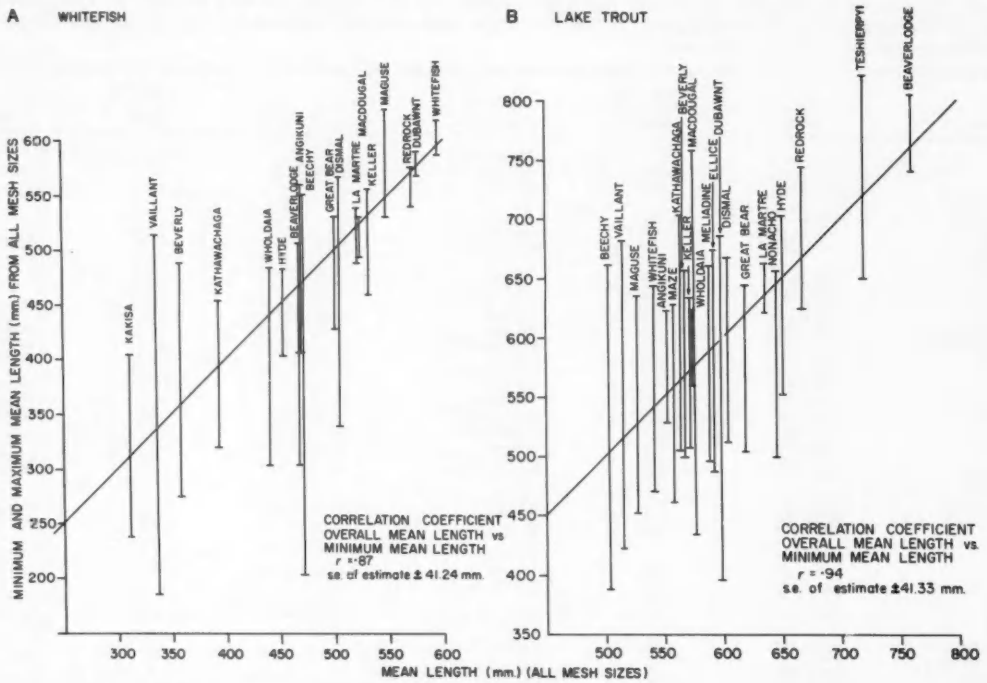

FIG. 10. Correlation between the mean length of fish caught in all mesh sizes and the smallest mean length of fish taken in any mesh size (usually 1½-in. mesh) for A, lake whitefish, *C. clupeaformis*, and B, lake trout, *S. namaycush*.

TABLE 4. Total number of fish caught by each mesh size for lake trout (*S. namaycush*) and lake whitefish (*C. clupeaformis*). Also score of number of length groups in which fish were caught, by mesh size (e.g. one set of a single mesh size capturing fish in five different 50-mm length groups scores 5). Data from Fisheries Research Board Barren Ground Survey 1959.

	Lake trout					Whitefish				
Mesh size (*in.*)	1½	2½	3½	4½	5½	1½	2½	3½	4½	5½
No. of length groups captured	251	249	218	199	201	109	107	97	89	85
No. of fish caught	695	921	1068	1229	889	594	1105	1535	1621	1370

681,000 kg of trout and whitefish was captured for a total removal of 3.8 kg per ha. The population has thus been subjected to some modification in the interval between samplings. Bond used a slightly different series of mesh sizes in Lac la Martre compared with those used in 1959; he substituted 6½-in. mesh for the 5½ in. previously employed; this was to conform with the practice of the local fishermen who can sell profitably only large whitefish. In spite of the relatively heavy fishery there is remarkably little difference in the length distributions of either whitefish or lake trout (Fig. 3 and 4). There is an increase in the numbers of small whitefish taken in the small mesh sizes in 1972 but this is not apparent for the lake trout; apart from this the shape of the distributions is identical in each one of the 2 yr.

The lake trout of Angikuni were sampled in

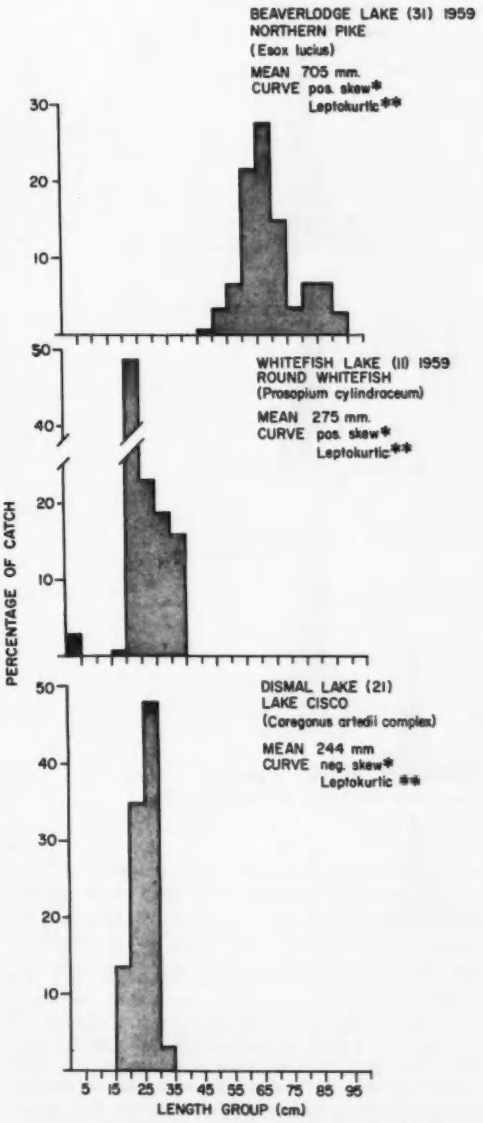

FIG. 11. Length-frequency distribution, all mesh sizes combined, for A, northern pike, *Esox lucius*, from Beaverlodge Lake 1959; B, round whitefish, *Prosopium cylindraceum*, from Whitefish Lake 1959; and C, lake cisco, *C. artedii*, from Dismal Lake 1959.

1959 using standard gangs (Fig. 5) and again in 1968, using only 5½-in. mesh. The results of the 5½-in. mesh in 1959 are compared with those of 1969 in Fig. 15. The difference in the results

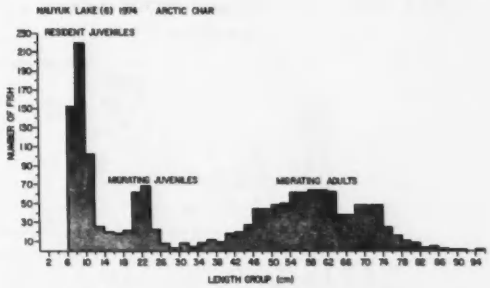

FIG. 12. Length-frequency distribution of Arctic char, *S. alpinus*, from Nauyuk Lake. Migrating adults and migrating juveniles taken at the counting fence on downstream run in 1974, resident juveniles taken during migration downstream from spawning lake in the same year.

of these samplings is small when it is recognized that the 5½-in. mesh is not the most efficient and captures the narrowest range of length groups (see section above); in fact, it is probably the worst mesh size for comparative purposes of all those employed.

Keller Lake was studied in 1962 (Johnson 1972) and again sampled briefly in 1974 (Table 5). The whitefish are remarkably constant in size between the time of the first sampling and the second fishing in 1974. The figures for the lake trout are not in such good agreement but they do not indicate any positive change when the small size of the sample in 1974 is considered.

Keyhole Lake was fished intensively by Hunter (1970) between 1961 and 1967; the greatest catches were in 1963 and 1965 and it was estimated that the equivalent of close to 100% of the initial stock was removed. The initial condition appears to be unimodal with a modal value of 308 mm (Fig. 7) but there is evidence that a smaller mode existed: Hunter in a personal communication states that "electrofishing in Keyhole Lake resulted in large catches of small to 20 cm fish." The initial fishing was sufficiently heavy to cause a change in the size and age structure. By 1965 the remnants of the initial population have grown slightly and may be observed in the right-hand peak in Fig. 7, while the left-hand peak consists of fish not showing in the earlier sample. These "new" fish are mainly in the 5- to 8-yr-old age-classes, while the 1963 peak at 9 yr old can be observed at the age of 11 yr in 1965. It is apparent that the "new" fish were present in the lake in 1962 as 2–5-yr-olds but too small to be taken by the gillnets. Thus, the reduction in the large population appears to have resulted in an upsurge of juveniles.

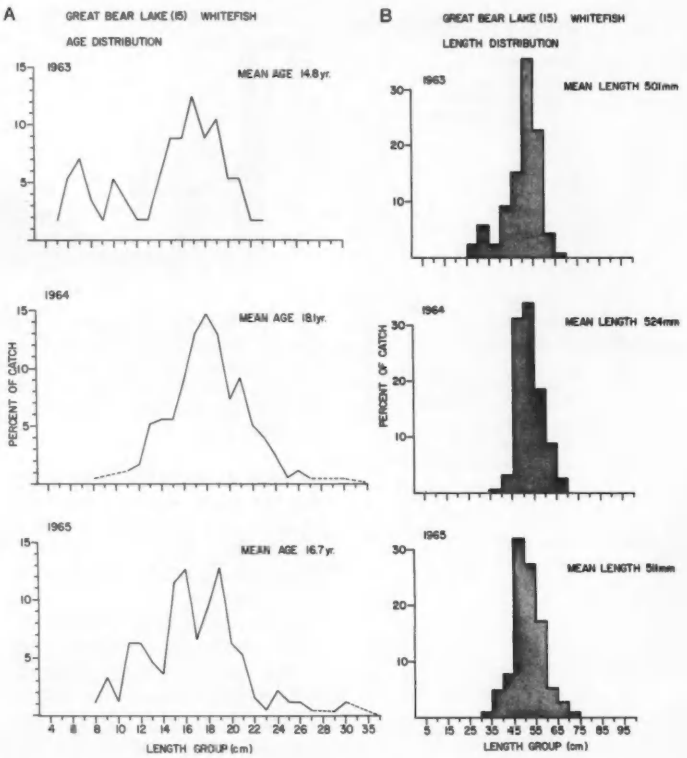

FIG. 13. Age- and length-frequency distributions of lake whitefish, *C. clupeaformis*, in Great Bear Lake for the years 1963–65, all mesh sizes combined.

Ten years later in 1975 (Fig. 7) the population has reverted to a condition very close to that of the original one; the char in the size range 170–250 mm have been eliminated as a significant group and two peaks have reestablished themselves with modal values at 111 and 314 mm. In addition to returning to a size structure very close to the original one the length–weight relationship is virtually unchanged:

1962–63	$\log W = 3.0236 \log L - 2.0461$
1975	$\log W = 2.95412 \log L - 1.9635$

Lake Namaycush was revisited in 1975 after a lapse of 13 yr (Fig. 7). Some differences in population structure can be observed, but in all probability these can be attributed to the sampling in 1962, which is now recognized as being unrepresentative. In this year only the shallow western end was sampled; no spawning fish were taken the majority being extremely large and probably senile. In 1975 the whole lake was explored more effectively and spawning fish in some number were captured; these were not in the largest size-groups. In both years the fish were extremely emaciated with heads of tremendous size. The length–weight ratio has remained virtually unchanged:

1962	$\log W = 2.62861 \log L - 3.95596$
1975	$\log W = 2.66830 \log L - 4.05757$

Relationship between age and size — In all northern populations it has been shown that there is a great range in age for fish of a given length (Grainger 1953; Miller and Kennedy 1948; Johnson 1972), and this condition has also been observed in other populations of considerable age, for example, the eel *Anguilla anguilla* of the English Lake District (Frost 1945). It is undoubtedly a widespread condition among fishes. In the populations at present being examined the majority of the fish occupy a relatively narrow length range, up to 60% falling within a single

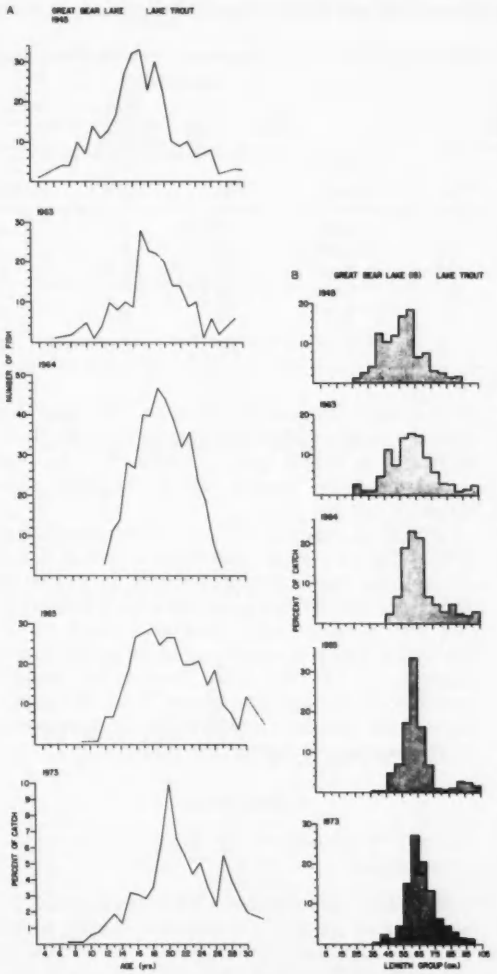

FIG. 14. Age- and length-frequency distributions of lake trout, *S. namaycush*, for the years 1945, 1963–65, and 1973. Data for 1945 from Miller and Kennedy (1948) and for 1973 from Falk et al. (1974); 1945 data from cotton nets, 1963–65 nylon nets, and 1973 from the sports fishery.

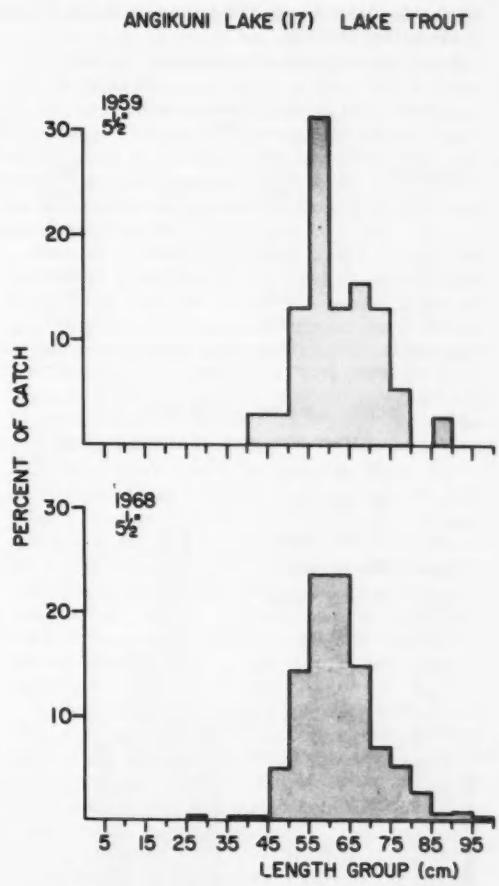

FIG. 15. Length-frequency distribution, for the 5½ in. mesh nets only, from Angikuni Lake in A, 1959 and B, 1968.

50-mm size-group; within such a length group ages may vary greatly. Obviously, the forces on the individual to achieve and retain a certain size are much greater than the tendency for the fish to increase regularly in length with time, i.e. there is little evidence for a regular growth pattern. Three examples, the whitefish of Beverly Lake (Fig. 16), the lake trout of Great Bear Lake (1963–65) (Fig. 17), and the lake trout of Lac la Martre (1959) (Fig. 4) will be considered.

In Beverly Lake the most numerous whitefish length-group (400–499 mm) is composed of members between 6 and 26 yr of age; these ages embrace most of the sample (3–26 yr). The members of the 100-mm length-groups on either side of the most numerous group show no overlap in their ages (100–399 mm: 7–16 yr; 500–599 mm: 17–26 yr), but both these length-groups lie within the span of the 400–499-mm group. The trend to increasing length with age is thus only of a general nature.

The length frequency of lake trout from Great Bear Lake is plotted by individual age-classes in Fig. 17. There is some trend to increasing length with age up to 20 yr, but beyond this age there is no sign of general increase. The length distribu-

TABLE 5. Mean lengths (ML) of lake whitefish (*C. clupeaformis*) and lake trout (*S. namaycush*) captured in Keller Lake in 1962 and 1974.

	Whitefish				Lake trout			
	1962		1974		1962		1974	
Mesh size (*in.*)	ML (*mm*)	No.	ML (*mm*)	No.	ML (*mm*)	No.	ML (*mm*)	No.
1½	554	39	546	1	503	33	514	4
2½	528	187	540	3	555	143	511	3
3½	540	132	542	3	559	106	506	5
4½	543	135	575	6	579	154	522	4
5½	546	124	565	6	617	71	496	2
Combined	544	617	560	19	573	507	511	18

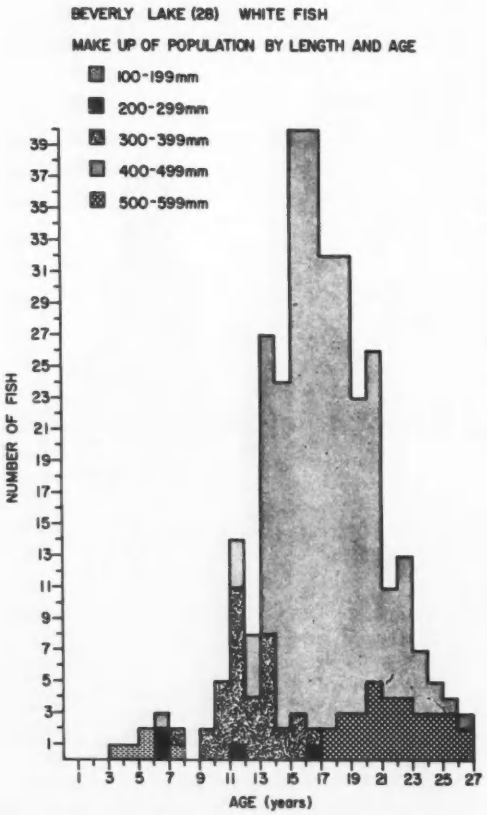

FIG. 16. The age-frequency distribution of lake whitefish, *C. clupeaformis*, in Beverly Lake 1959, by length groups. The relationship between age and length is general, the smallest fish being generally younger than the largest: the most numerous size-group 400–499 mm contains ages from 6 to 26 yr.

tion remains remarkably constant. This does not prevent certain individuals in any age-class from achieving a length greatly above the mean or conversely from lagging behind the mean class value at any age.

In Lac la Martre, the lake trout sampled in 1959 (Fig. 4) show one distinct group much larger than the majority. The fish in the more numerous smaller group are between 8 and 20 yr old with a modal value between 11 and 12 yr; the larger group is almost identical in age and is made up of 11–21-yr-olds. There is no bimodal structure to the age distribution. That the condition is not transient is shown by the appearance of the two distinct groups 13 yr later in 1972.

Discussion

Species Composition and Environmental Gradients

A well-marked gradient of increasing species diversity exists starting at northern Ellesmere Island (83°N) and moving south to the territorial boundary (60°N) and beyond; but there is also a gradient of increasing diversity from Baffin Island in the east to Victoria Island in the west. Such gradients are probably the result of an inextricable mixture of environmental conditions and accidents of distributional history; they are also based on a relatively small number of species.

The small complement of species in a given situation in the arctic compared with that of a similar one in temperate or tropical conditions has long been recognized; it was on this account that Wallace (1878), and more recently Fischer (1960) and Dunbar (1960a, b; 1968) have suggested that, from an evolutionary point of view, arctic systems are immature. This thesis was

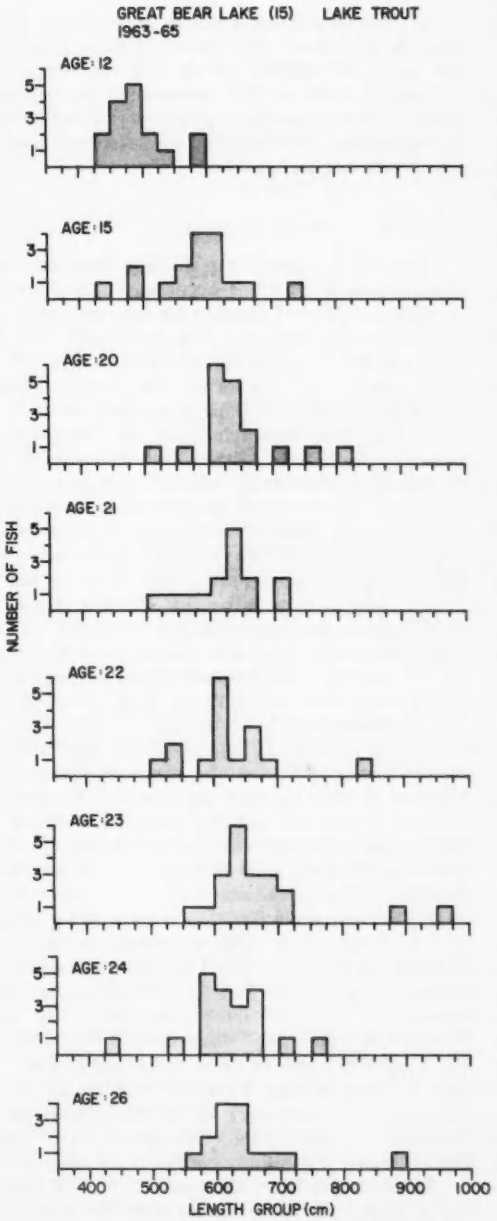

FIG. 17. Great Bear Lake, lake trout, *S. namaycush*, showing the gradual increase in modal length as age increases from 12 to 20 yr old. Beyond the age of 20 yr there is no increase in modal length.

rejected by Connell and Orias (1964) for lack of evidence and the problems entailed in obtaining confirmatory observations. It is questionable whether arctic systems have, in fact, had a short evolutionary history even though their existence in present locations is undoubtedly recent; there would seem to be no reason why they have not been able to migrate north and south in a manner similar to that suggested by Newell (1962) for more temperate biota.

A more fertile approach to understanding the individual species and the species interactions making up the total ecosystem is the study of gradients that can be more immediately related to environmental conditions. Vegetational analysis gradients have been shown to exist through time, leading to the equilibrium position of the climax (Tansley 1935, 1939; Whittaker 1953; Langford and Buell 1969) and space (Curtis and McIntosh 1951; Whittaker 1967). Species have been shown to change continuously in their abundance and growth form along lines of environmental change, changes in the status of individual species resulting in changes in the makeup of the communities. A climax is any well-marked enduring community which may persist indefinitely with relatively regular climatic conditions provided that there are no deterministic or organismic overtones as implied by Clements (1936).

Margalef (1968) equates maturity with diversity, a diverse system being more mature than one with fewer species. This, however, seems to be too broad a generalization, since mature forest may contain fewer species than the preceding successional stages (Whittaker and Woodwell 1972). Johnson (1975b) showed that fewer species existed in Great Bear Lake than in smaller lakes of comparable age within the same drainage basin. Low species diversity appeared to be the result of extreme environmental conditions. There also exist in the arctic, in regions of postglacial land uplift, at relatively low elevations above sea level, lakes that show less species diversity than lakes slightly below them and hence younger. Similarly two adjacent lakes at approximately the same elevation may each show a different species complex both of which appear to be derived from a condition that includes both sets. Little Nauyuk Lake (char dominated) and Klondike Lake (lake trout dominated) each have only a portion of the full species complement found in Nauyuk Lake (Table 1). Undoubtedly some species in each case have been eliminated by competition for the very short supply of resources; as in the forest climax a reduction of diversity is apparent compared with the earlier stages of

succession. Given time each lake matures to reach a climax condition individual to that lake.

With the objective of examining the possible existence of gradients in fish populations, the relative importance values (percent catch composition by weight) of lake trout and whitefish were arranged in order of their relative magnitude (Table 2, Fig. 2). The results indicate that there are lakes where only lake trout are present (although invariably one species of cisco, *Coregonus artedii*, *C. autumnalis*, or *C. sardinella*, is present with the lake trout), through lakes where there are equal proportions of trout and whitefish to those lakes (mainly outside the region being considered) that contain, of the two species being considered, only whitefish. There is, in fact, a well-marked gradient of changing species composition.

The proportions of lake trout and whitefish show no clustering about a specific value; this is indicative of the independence of the two species and the formation of independent communities in each lake or region within a lake. This independence is confirmed by the largely independent food chains of the two species and the rather remarkable absence of whitefish in the trout diet (Johnson 1972, 1975b). Evidence obtained through the comparison of Great Bear and Great Slave lakes indicates that it is largely the density of benthic food organisms that limits summer distribution of whitefish, and not temperature or depth. In the southern portion of its range whitefish inhabit the warmer, more productive lakes that lake trout are apparently unable to tolerate. Lake trout, by contrast, are able to withstand extremes of great depth, no light, and low temperature.

Whitefish and lake trout are terminal predators, each at the end of its respective food chain and each free of dependence on the other; both species eventually reach sufficient size to be entirely free from predation whatever the source. Both species live to a great age so that their populations reflect a "time-binding" character, or the embodiment in the population of the effect of past years' environments and interactions (Whittaker and Woodwell 1972). These fish populations thus appear to have the characteristics of the dominant species in a climax community. Whittaker and Woodwell contrasted forest and phytoplankton and concluded that it was difficult to apply the climax concept, as they had discussed it, to aquatic natural communities. In aquatic communities there may be a significant change of role between plant and animal so that fish in lakes dominate the structure of the community in a manner comparable with that of trees in the forest. This condition is not to be confused with the "biotic climax" of Tansley (1935), which is the term he applied to an arrested stage of succession, such as that maintained by grazing animals. In the aquatic situation it is a final stage of equilibrium, the so-called stable climax condition, which has been reached.

Equilibrium in Arctic Lakes

Since 1924 when Elton (1924) first showed that cyclical fluctuations occurred in the harvest of many northern Canadian fur-bearing animals, a considerable literature has developed (Elton 1934, 1942; Elton and Nicholson 1942; Vibe 1967) on animal cycles in the north. Cyclic fluctuations have become associated with the arctic; this has been reinforced by the conclusions of MacArthur (1955) that diversity leads to stability in tropical systems and hence, by contrast, arctic systems which are low in diversity are inherently unstable. More recently Krebs and Myers (1974) have shown that fluctuations in small mammal populations occur in many parts of the world irrespective of latitude. Clough (1972) has also reported the existence of a stable community of hutias (*Geocapromys ingrahami*) existing in a tropical island setting and having very low diversity of both plants and animals owing largely, to the low rainfall.

Johnson (1972, 1973) suggested that unexploited fish populations in northern lakes are constant in their age and size structure over long periods of time without any evidence of fluctuation, a conclusion also reached by Dunbar (1973) on the basis of work by Grainger (1953) and his own long arctic experience.

If arctic populations of fish show a steady state over long periods of time, is it possible to refer to them as being stable? The literature on this subject suffers from lack of differentiation between the terms "stable" and "being in an equilibrium condition." Margalef (1963, 1968) has suggested that the ratio of primary production to mean annual biomass (P:B ratio) is a measure of the stability of an ecosystem, and MacArthur (Leigh 1965) has pointed out that dimensionally this ratio is similar to the reciprocal of the mean life span: the smaller the P:B ratio (or 1/mean life span) the greater the stability. This index was developed for whole ecosystems, but by the same reasoning the relationship of the energy entering an individual species through its food supply in relation to the biomass of that species would be a measure of its stability. Hurd et al. (1971) developed a different measure of stability based on thermodynamic considerations,

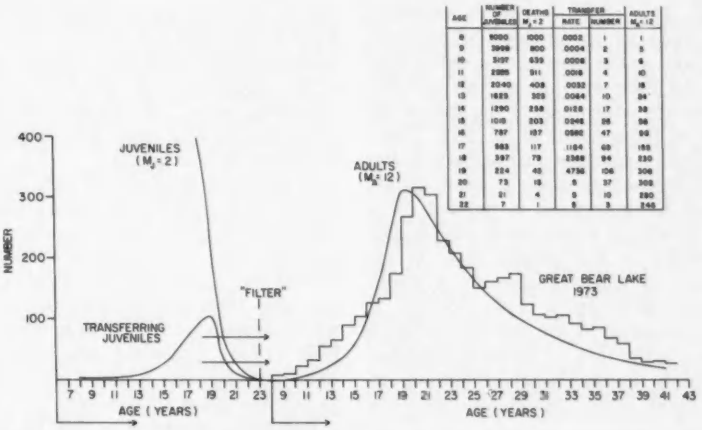

FIG. 18. A possible mechanism whereby a constant modal age is maintained in the catchable portion of the population. Fish from a juvenile group are allowed to pass to the "establishment" as mortality in this group reduces pressures on the juveniles. Recruitment through the "filter" or suppressive mechanism of adult on juvenile is over a 15-yr span (from 8 to 23 yr); it is low at 8 yr and reaches a peak rate at 19 yr. The smooth curve represents the theoretical passage of a single year-class through time, and the histogram the actual age-frequency distribution of the angling catch in Great Bear Lake in 1973. Data for the angling catch from Falk et al. (1974) smoothed by 3s.

which requires that a stable system is one characterized by 1) the rapidity of the response to perturbation, 2) the amplitude of the deflection from the ground state, and 3) the rate at which the perturbation is damped.

Consideration of these definitions leads to the conclusion that the P:B ratio is an indication of the existence of a steady state, whereas application of the criteria of Hurd et al. provides information on the real stability of the system, or the force required to move the system from the equilibrium position. The P:B ratio is a measure of the persistence of the ecosystem in the face of the environmental conditions experienced over its lifetime; it provides no information on the stability unless information on the environmental conditions experienced is also given.

The invariably high mean age of the arctic fish populations sampled indicates the long-term existence of a state close to the equilibrium, or climax, condition. The fact that all populations appear to be in the same phase indicates that this condition exists indefinitely; if this were not the case it might be exepcted that fluctuations would be apparent in at least one or two lakes. The steady state is epitomized by Great Bear Lake where the rate of turnover in the adult population alone is 17.3 yr, and this does not include the period of 8–20 yr that these adults spend in the prerecruit phase (Fig. 18); these conditions have remained constant over 30 yr. In Lac la Martre conditions have remained constant over 12 yr, in Lake Namaycush over 13 yr, and in Angikuni over 10 yr; there is no evidence to indicate periodic fluctuations in these fish populations. Even in Vaillant Lake, the whitefish population, which by its size structure might be considered to be undergoing a recovery process, is shown by its age structure (mean age 18.9 h) to have been in this condition for a long time.

From a qualitative point of view primary production in arctic lakes is very low, being <8.5 g $C \cdot m^{-2} \cdot y^{-1}$ (Kalff 1970; Hobbie 1973), but total biomass is high. Hunter (1970) estimated the total biomass of char to be 48.8 kg/ha for Char Lake. Lac la Martre gave catches of 79 kg/100 m of net per 24 h and in the most favorable regions of Great Bear Lake 81 kg of trout and whitefish/100 m of net per day were obtained. Undoubtedly a very high biomass is present compared with primary production.

The only evidence for the magnitude of the forces inducing equilibrium is provided by Keyhole Lake. After a heavy fishery in 1962–63 and 1965 in which a large fraction of the initial population was removed, recovery was complete 10 yr later in 1975. Unfortunately, it is not known for how long prior to 1975 recovery had

been achieved. The early stages of recovery (1965) are marked by an upsurge of juveniles present in the lake at the time of the initial fishery (as shown by their age); these fish in 1962 were presumably the equivalent of the fish in the left-hand mode of those captured in 1975. There appears to be little oscillation in numbers as the juveniles move forward to assume adult status. The recovery of Keyhole Lake is marked by a rapid response to a large perturbation and a high degree of damping as the ground state is regained, the essential characteristics of a stable population as defined by Hurd et al. (1971).

There is little doubt as to the essential stability of Keyhole Lake in the face of massive perturbation and its ability to regain and maintain an equilibrium position when extraneous perturbations are removed.

The second lake meriting careful scrutiny is Nauyuk Lake. There is no possibility here that the bimodal distribution of the seagoing population is caused by gillnet selection as all records were obtained at the counting fence. That the population is in equilibrium is demonstrated by the high percentage of tag returns and the virtually constant size of the population between the 2 yr.

The structure of the Nauyuk Lake char population is almost identical with that observed by Grainger (1953) in the Sylvia Grinnell system, Baffin Island.

Completely independent evidence for the ability of arctic ecosystems to maintain a steady state condition is provided by Rigler et al. (1974) who showed that the crustacean plankter *Limnocalanus macrurus* remained at quite constant numerical strength over a 4-yr study at Char Lake (75°N), Cornwallis Island.

From these considerations relatively simple systems can apparently exist in equilibrium and also exhibit a considerable degree of stability. This seems contrary to the conclusions of MacArthur (1955). Margalef (1968) considered that stable systems at low temperature might have existed at one point in the earth's history but that they were no longer present.

Age and Length Distribution of a Population in Equilibrium

Frequency distributions of fishes in unexploited arctic lakes all show similar patterns of size and age; the characteristic form shows one or more bell-shaped curves that approach a Gaussian or normal distribution. A high degree of clustering around the modal value is characteristic for length but this is less marked for age. If these curves are truly representative of the populations from which they are drawn, how is it possible to reconcile them with the virtually static condition of the population? It will be shown that such a "standing wave" for length and age is in fact characteristic of a population limited by resources to a fixed establishment.

It has been known for some time that unexploited fish populations often show an extreme condition in which large numbers of old fish of uniform size exist. Baranov (1918) was first to discuss this condition; he provided the explanation that there was an accumulation of old fish whose growth decreased proportionally with age. Hart (1931) examined populations of whitefish from Shakespeare Island Lake which appeared to confirm these suggestions.

Baranov's reasoning is not, in itself, sufficient to explain the existence of what Ricker (1975) has termed the "dome-shaped" catch curve, which is a relatively symmetrical curve about a point where fish of a certain length are caught in greatest abundance and where frequency of capture declines on either side. There appear to be two possible explanations for the left-hand ascending limb of the curve. The first is that the fish are not fully vulnerable to the gear being employed and are, therefore, under represented in the catch in proportion to their actual abundance in the lake. This is the explanation usually invoked and has gained almost universal acceptance (Grainger 1953; Beverton and Holt 1957; Ricker 1975; Kennedy 1953). This explanation based on reduced vulnerability stems from the assumption that there is a mean size roughly correlated with age and that this growth pattern is relatively constant for a given water body. If growth is regular and year-class strength relatively uniform, then the numerical strength of each length-group will decrease as length increases, following a negative exponential function similar to that for mortality; catch curves for age and length will then be quite comparable. If year-classes are not numerically uniform then it might be expected that there would be numerous size-groups, which, owing to slightly different growth rates, would tend to become obscure, but that such discontinuities would show up in the catch curve for age. Neither condition provides a satisfactory explanation for the regularly ascending left-hand limb of the catch curves observed; ultimately, it is necessary to decide between an explanation involving reduced vulnerability or an explanation involving an irregular growth pattern.

The alternative explanation is that the catch curve is not an artifact of the sampling procedure but does represent the population in the lake over

most of the lengths sampled. If it is assumed that the number of adult fish in a lake is constant, as appears to be the case from analysis of age and length, then recruitment must be controlled, most probably through a feedback mechanism that dampens fluctuations in year-class strength, if this occurs, and admits only such recruitment as is necessary to achieve equilibrium with mortality. In these circumstances it is necessary to postulate an increase in growth rate (not necessarily tied to a certain chronological age since recruitment occurs over a number of years) as soon as a fish moves into the phase of active recruitment.

There are several arguments that support the second alternative rather than the first. In the first place the modal size of fish in the catch curve varies from lake to lake in such a way as to require great changes in vulnerability to account for it. These changes in vulnerability would all have to move in concert for all the five different mesh sizes in the standard gang as shown in Fig. 3–5. It would be necessary to postulate that, using identical gear, lake trout smaller than 745 mm are not fully vulnerable in Beaverlodge Lake although fully vulnerable at 486 mm in Vaillant Lake. Similarly char become fully vulnerable at 150 mm in Gaviafaeces Lake, 220 mm in Little Nauyuk Lake, 320 in Keyhole Lake, while in Lake Namaycush, lake trout only become fully vulnerable at 765 mm.

The clustering of fish in the population curve around a certain length value, with this clustering being evident in all mesh sizes, makes it impossible to believe that these are samples from a population in which numbers decrease regularly with size, or that smaller sizes are not showing up because of reduced vulnerability at least above 250 mm for the standard gang or 100 mm for the experimental nets.

The counting fence at Nauyuk Lake does not have the assumed disadvantage of selectivity but the population of seagoing fish shows a well-defined bimodal structure.

If the samples described are representative of the populations from which they are drawn and these populations are in a steady state or climax condition, it is necessary for full understanding to provide a mechanism for population control through a feedback system and then to describe a model of the manner in which the system works.

The Feedback System

In a forest climax young trees are suppressed by the exclusion of light at lower levels through the formation of a closed canopy; this canopy is a property of the assemblage of dominant trees but not the individuals. In a comparable manner it is suggested that corporate action of the adult portion of the dominant fish population maintains the juvenile mode in a peripheral position through some suppressive force.

The evidence for suppression is to be found in the bimodal structure of the populations from Keyhole, Namaycush, and Nauyuk lakes. In the first two lakes juveniles were found mainly along shorelines and tributary streams; in Nauyuk Lake the juvenile mode moved seaward only after the completion of the main adult run (Johnson and Campbell 1975). In Little Nauyuk and Gaviafaeces lakes, possibly also in Fiona Lake, the juvenile mode appears to be suppressed entirely apart from an ephemeral mode that would exist for a brief time after hatching. Cannibalism may play some part in the suppressive process; de March reports (personal communication) that most of the large char taken in Fiona Lake in 1975 had small char in their stomachs; Johnson (1975a) reported 2.8% cannibalism in lake trout in Great Bear Lake; however, it is felt that this is not the main mechanism, as cannibalism has not been observed in the majority of char or lake trout populations and never in whitefish. The restriction of juveniles to the periphery would tend to increase predation by birds when the population rose above the available niche space, the "nook-an-cranny" effect of Smith (1972).

When mortality in the established population reduces its ability to maintain juveniles in the peripheral zone, opportunities are created for the smaller fish to move forward, go through a period of rapid growth, and achieve establishment status. This process has the characteristics of an electronic filter in reducing "noise" or, here, recruits in excess of those necessary for replacement. Such a mechanism would tend to favor vigor as well as opportunity in a manner exactly comparable to the openings provided to seedlings or saplings in a forest; when a break in the canopy occurs, recruits move forward to occupy the space available.

The high degree of clustering around the modal size, although this size may be achieved over a wide span of ages, indicates that growth of individuals does not increase regularly with time. A plateau may be reached early or late in life, from which time onward size may remain stationary for a period; this is well illustrated by Beverly Lake whitefish (Fig. 16), Great Bear Lake trout (Fig. 17), and the direct observation of tagged lake trout in Great Bear Lake that did not grow appreciably over an 8–10-yr interval. These examples not only indicate nonuniform growth

rates, but the existence of certain constraints on size, as if individuals represent nodes of equipotential in superimposed fields of force, one of the fields of force being the interaction between individuals.

A closely parallel condition has been observed in the predatory fish populations of Lake Tanganyika (Coulter 1970); data collected during purse-seining in the offshore waters for the small clupeid fishes *Limnothrissa miodon* and *Stolothrissa tangenicae* are remarkably similar to those from northern lakes. Three of the predator species *Lates mariae*, *L. microlepis*, and *L. angustifrons* are all shown to have a high degree of clustering around the modal value in the unexploited state: *L. mariae* has a modal length of about 600 mm, *L. microlepis* 700 mm, and *L. angustifrons* about 750 mm. Smaller modes of these species are found along the littoral regions of the lake at lengths between 50 and 180 mm. Coulter considers that, especially for *L. microlepis* and *L. angustifrons*, the catch curves for the pelagic populations represent the actual size distributions fairly closely. Aging was not possible as no check marks occur in tropical fishes.

Model of a Fish Population in Equilibrium

A model of a fish population in a steady state has been developed for the Great Bear Lake lake trout population (Fig. 18). There is a wide range of ages in the juvenile mode, only the descending limb of which is shown. A given year-class will reach the earliest age at which it is possible for young trout to make the transference (age 8 yr in the model) to the establishment. As size of some individuals increases with time additional juveniles make the transference at successive ages until a peak rate at transfer is achieved (age 19 in the model); the rate of increase in the probability of any fish making the transference has been considered to be exponential until a maximum transfer rate of 0.5 occurs at the age of 20 yr; by this time numbers in the juvenile phase of the year-class have declined to a very low number, although at peak abundance in the adult phase. The juvenile segment becomes extinct at the age of 23 yr. The adult phase accumulates a given age-class up to the age when it reaches 20 yr after which mortality in the adults is greater than recruitment so that numbers begin to decline. Mortality rates of 20 and 12% have been applied annually to the juvenile and adult groups, respectively.

This model provides a close fit to the actual population data from Great Bear Lake as given by Falk et al. (1974). In the model Falk's results are shown in the histogram, while the computed results are shown in the smooth curve. The model does not violate, in any way, the "law" of mortality which requires that the number in an age-class must always decrease with time. It is only in the adult mode where numbers in a given year-class do appear to increase, but here only a fraction of the total existing year-class is represented. Growth calculated from adult catches will give a biased view of the growth of the year-class as a whole, since only the fastest growers will be included.

This model may be contrasted with that developed by Coale (1972) for a human population in equilibrium. In Coale's model birth rate is in balance with death rate but there is no feedback mechanism to control birth rate in the face of changing death rate. Such a model would have no built-in stability with which to resist perturbation; fluctuations in birth rate would be reflected through the population, while changes in death rate would reduce or augment the adult population. Coale's model does emphasize the present human dilemma but does not meet the constraints on fish populations that have reached the limit of the finite resources available to them.

There are two aspects to the feedback model that seem to be most satisfactory from an ecological viewpoint, particularly in conditions where resources are scarce. In the first place it is much more efficient as the majority of the energy entering a species in a steady state is directed to maintaining a large number of large adults, rather than toward the production of a large number of prerecruits which would, in effect, serve merely as energy gatherers for predators of other species, i.e. the greater part of the mortality takes place when the fish are small (even if quite old). The second feature is the great ability of the system described to absorb year-to-year fluctuations in year-class strength; if the juvenile population is depleted through several years of poor hatching or early development, it is quickly refurbished with the advent of a good year. The juvenile group is a reservoir from which recruits are drawn as necessary.

Feedback Model in Other Biological Situations

If the model described has validity in arctic lakes then it might be expected to be found in circumstances which are to a degree comparable. Reference has been made to similarities between the dominant fish species and dominant forest trees. It is here that one might expect to find the closest comparison in size and age structure.

It is difficult to find examples of truly untouched forest on which the necessary measurements have been taken; Jones (1945) gives examples of size composition by stem diameter for European forests and McIntosh (1972) and Buell and Carlton (1951) for North America. Jones, who doubts the existence of truly virgin forests in Europe, unmodified by fire, animal grazing, or cutting stresses the fact that stems of small diameter are often rare in a climax forest so that judged by the uniformity of trunk size the stands appear to be evenly aged.

Many forests, with little diversity in the species making up the canopy, have achieved an equilibrium condition, stable over many thousands of years in the face of the natural perturbations they have had to withstand. This stability may have been manifested through an annual climatic cycle of great variation as in the Douglas fir (*Pseudotsuga menziesii*) forests of the Pacific coast of Canada and the northern part of the United States.

The bell-shaped age and size structure of populations in the equilibrium condition, far from being unusual, is what might be expected when the four following conditions are fulfilled: 1) a fixed establishment; 2) entry not fixed at a specific age but occurring over a spread of years; 3) potential recruits exceed those accepted; 4) numbers in the establishment are sufficient to ensure a reasonably constant mortality, and hence, recruitment.

These conditions are frequently encountered in human social groupings such as in certain legislative bodies (e.g. Canadian Senate or British House of Lords where group renewal does not depend on election at fixed intervals), professional sports teams, and other social groups with a fixed establishment. In these circumstances age and size (length or weight) will follow nearly Gaussian distributions and these will remain constant with time.

Implications for Fisheries Management

The existence of a gradient in the ratio of the relative importance value of lake trout and whitefish in a community emphasizes the need for conducting fisheries or other surveys in the field of aquatic biology through examination of environmental gradients. Surveys should be planned with the existence of gradients in mind. The nature of the gradient to be explored will depend on the circumstances of the survey but gradients may be found within lakes, through changing elevation, or across geological boundaries; latitudinal gradients are likely to be less profitable. As Whittaker (1967) maintains "gradient analysis has changed the concept of vegetation as much as research on the genetic basis of variation and evolution has changed the concept of plant species." Gradients in lake populations may be more difficult to explore and analyze than plant communities, but certainly the rewards could be as great.

Recognition of the fact that the dominant fish populations in northern lakes are in a steady state or climax condition implies the existence of a degree of homeostasis and therefore, according to Tansley (1935) and Baker (1966), a degree of organization. This organization can be discerned in the shape of the length and age distributions and in the clustering around a modal length value. The independence of each organizational unit (or lake) is shown by the different modal sizes and ages and in the proportion of each species present.

Any fishing pressure on a climax condition will tend to reduce the level of organization by increasing the energy flux through the system and producing a concomitant loss of equilibrium. With increasing pressure the system is strained to the point where the dominants can no longer exert any form of corporate control so that oscillations, triggered perhaps by small changes in the environment, are set up. A single species of fish, as in the char of Keyhole Lake, will return rapidly to the equilibrium position, whereas a more complex system will have many alternative pathways through which the energy can move. Therefore, the chances are greater for oscillations to develop before equilibrium is reestablished (May 1973). In Canadian freshwater fisheries it is usually the dominant species that are sought after; it is therefore essential to think in terms of sustained populations rather than sustained yields.

A singular characteristic of the dominant species has been shown to be that, in the final prerecruit stage, it must control its own recruitment. If the dominance is destroyed, what is the effect on the juvenile groups? Can they out-compete subordinate species without some form of parental presence, albeit of a repressive nature, or do they require a parental "canopy" for their proper survival? Production may be limited by the failure of the juvenile group to reestablish itself following initial replacement of a harvested population. The "fishing-up" process attempts to speed up the energy flow through the system and maintain a regular succession of ages and sizes through the fishery, but in Great Slave Lake, in spite of high initial abundance, lake trout were virtually eliminated from the Western Basin with

no signs of a upsurge of small young fish (Keleher 1972). Evidently lake trout have evolved toward low replacement rates or K-selection (MacArthur 1972) to such an extent that they can only maintain a large biomass at an extremely low turnover rate. Char and whitefish have undoubtedly a much greater resilience to harvesting, and there is little doubt that the now decimated char populations of Greiner and Sylvia Grinnell lakes would recover rapidly if cropping were suspended. Traditionally the Eskimo fished char on an intermittent basis, moving to a new system when the run being fished was reduced to a low level of harvest, returning to the original fishery only after a lapse of several years. Rotational fishing of a slow-growing climax population seems to have much to commend it.

If the desired goal of lake fisheries management is the regulation and maintenance of a fishable population of large fish, then it is essential to determine the status of fish in the intermediate size range. In the bi- or multiple-modal model there will be a relatively small group of fish of this size, fast-growing and probably feeding voraciously and hence quite vulnerable; it is upon these fish that adult replacement will depend and it is essential that they be given maximum protection. If, on the other hand, the theory in which numbers decrease with size is valid then this intermediate group will be relatively abundant and will need little protection. Every effort should be made in any management program to ascertain the status of the postrecruits and to protect them accordingly.

The turnover time of a population will also provide most useful information on the state of a fishery. The turnover time ($\overline{T}$) is, in effect, the reciprocal of the P : B ratio and may be calculated:

$$\overline{T} = \frac{1}{N} \sum_{i_{min}}^{i_{max}} (T_i)(f_i)$$

where T_i = age of animal; f_i = number of animals in age class i; and i_{min} and i_{max} are the maximum and minimum ages in the catch. Changes in turnover time, being relative, will be less influenced by aging error than absolute values.

It will be seen from the foregoing that fish populations in lakes have evolved under different conditions from those in the sea. Lakes with their finite bounds have contained the incoming energy and evolved toward the establishment of dominance and the maintenance of the steady state, while the oceans with their fish populations living in a state of continuous instability (Longhurst et al. 1972) have had to solve a different set of environmental equations. Results from one set of circumstances should only be transferred to the other with a degree of caution.

Although it is arctic lakes that have been considered in this paper they do not appear to be greatly different in type or in species complex (apart from the presence of Arctic char) from those farther south. Most Canadian lakes east of the Rocky Mountains were originally dominated by whitefish and/or lake trout and, if the early reports are to be believed these species were present in great abundance and were of uniform size. Most populations have failed to withstand heavy exploitation. Perhaps management authorities and fishery scientists have been influenced too greatly by brilliant mathematical analyses and paid too little attention to the underlying ecology and the understanding of ecological processes which are often too variable and too complex to be satisfactorily represented mathematically.

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Parasites of Fishes of Aishihik and Stevens Lakes, Yukon Territory, and Potential Consequences of Their Interlake Transfer Through a Proposed Water Diversion for Hydroelectrical Purposes

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ARTHUR, J. R., L. MARGOLIS, AND H. P. ARAI. 1976. Parasites of fishes of Aishihik and Stevens lakes, Yukon Territory, and potential consequences of their interlake transfer through a proposed water diversion for hydroelectrical purposes. J. Fish. Res. Board Can. 33: 2489–2499.

Forty-six species of parasites (14 Protozoa, 7 Monogenea, 7 Digenea, 8 Cestoda, 2 Acanthocephala, 4 Nematoda, 3 Copepoda, and 1 Hirudinoidea) were recovered from 383 specimens of 8 species of fishes collected from Aishihik and Stevens lakes, Yukon Territory, during the summer of 1973. Four species, *Chloromyxum dubium* Auerbach, 1908, *C. esocinum* Dogiel, 1934, *Sphaerospora cristata* Shulman, 1962 (all Protozoa), and *Crepidostomum metoecus* Braun, 1900 (Digenea) are reported for the first time from North America.

Aspects of the systematics and distribution of several species are discussed and the following new synonymies recognized: *Tetraonchus rauschi* Mizelle and Webb, 1953 with *T. borealis* (Olsson, 1893) (Monogenea); *Cystidicola stigmatura* (Leidy, 1886) with *C. farionis* Fischer, 1798; and *Raphidascaris canadensis* Smedley, 1933 with *R. acus* (Bloch, 1779) (both Nematoda).

Substantial differences in the parasite fauna of Aishihik and Stevens lakes are noted; the possible consequences of the introduction of species of potential economic and pathogenic importance e.g. *Henneguya zschokkei* (Gurley, 1893), *Hexamita salmonis* (Moore, 1923) (both Protozoa), *Discocotyle sagittata* (Leuckart, 1842) (Monogenea), *Neoechinorhynchus rutili* (O. F. Müller, 1780) (Acanthocephala), and *Triaenophorus nodulosus* (Pallas, 1781) (Cestoda) into new areas as a result of the proposed diversion of Stevens Lake (Yukon River system) into Aishihik Lake (Alsek River system) are discussed.

ARTHUR, J. R., L. MARGOLIS, AND H. P. ARAI. 1976. Parasites of fishes of Aishihik and Stevens lakes, Yukon Territory, and potential consequences of their interlake transfer through a proposed water diversion for hydroelectrical purposes. J. Fish. Res. Board Can. 33: 2489–2499.

Quarante-six espèces de parasites (14 Protozoa, 7 Monogenea, 7 Digenea, 8 Cestoda, 2 Acanthocephala, 4 Nematoda, 3 Copepoda et 1 Hirudinoidea) ont été recueillies de 383 individus appartenant à 8 espèces de poissons capturés dans les lacs Aishihik et Stevens, Territoire du Yukon, au cours de l'été 1973. Pour quatre espèces, *Chloromyxum dubium* Auerbach, 1908, *C. esocinum* Dogiel, 1934, *Sphaerospora cristata* Shulman, 1962 (tous Protozoa) et *Crepidostomum metoecus* Braun, 1900 (Digenea), il s'agit de premières mentions en Amérique du Nord.

Les auteurs discutent de certains aspects de la systématique et de la répartition de plusieurs espèces et reconnaissent les nouvelles synonymies suivantes : *Tetraonchus rauschi* Mizelle et Webb, 1953, synonyme de *T. borealis* (Olsson, 1893) (Monogenea); *Cystidicola stigmatura* (Leidy, 1886) synonyme de *C. farionis* Fischer, 1798; et *Raphidascaris canadensis* Smedley, 1933, synonyme de *R. acus* (Bloch, 1779) (tous deux Nematoda).

On note d'importantes différences dans la faune parasitaire des lacs Aishihik et Stevens; on examine les conséquences possibles de l'introduction d'espèces d'importance économique et pathogène potentielle (e.g. *Henneguya zschokkei* (Gurley, 1893); *Hexamita salmonis* (Moore, 1923) (tous deux Protozoa); *Discocotyle sagittata* (Leuckart, 1842) (Monogenea); *Neoechinorhynchus rutili* (O. F. Müller, 1780) (Acanthocephala); et *Triaenophorus nodulosus* (Pallas, 1781) (Cestoda) dans de nouvelles régions comme résultat du détournement proposé du lac Stevens (réseau du fleuve Yukon) vers le lac Aishihik (réseau de la rivière Alsek).

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THE Northern Canada Power Commission's proposals for the Aishihik Lake Hydro Power Development in the Yukon initially included diverting Stevens Lake at the headwaters of the Yukon River system (draining into the Bering Sea) into Aishihik Lake at the headwaters of the Alsek River system (draining into the Pacific Ocean). Among other biological problems arising from hydroelectric developments on Aishihik Lake, this proposed water diversion raises the possibility of the transfaunation of detrimental fish parasites between these two lakes and throughout the lower reaches of the Alsek River system.

Because of the lack of knowledge of the parasite fauna of fishes of this area and the possibility of introducing potentially harmful species into new aquatic environments, a survey of the parasites of fishes of Aishihik and Stevens lakes was undertaken during the summer of 1973. This study was part of a series of biological, engineering and socioeconomic investigations conducted by Environment Canada's Fisheries and Marine Service in an attempt to assess and resolve fisheries resource problems associated with hydroelectric developments at Aishihik Lake. The primary objective was identification of the parasites present in the two lakes and assessment of possible dangers due to parasite transfaunation.

The parasite fauna of fishes of the far northwest of North America is poorly known. There are fewer than 30 papers dealing in whole or in part with parasites of anadromous and freshwater fishes of Alaska, northern British Columbia, and the Yukon Territory. Only five papers (Wilson 1908, 1915; Clemens et al. 1945; Schmidt 1965; and Dunagan 1957) record parasites of fishes of the Yukon River drainage, and prior to the present study no published records were available for the much smaller Alsek River system. Based on material obtained during the study reported herein, Arthur and Margolis (1975a, b) dealt with the systematics and zoogeography of the nematode *Haplonema hamulatum* Moulton, 1931 and described a new species of the myxosporidan genus *Myxobilatus* from Aishihik Lake.

Materials and Methods

The two lakes studied are located approximately 160 km northwest of Whitehorse. Aishihik Lake (61°28′N, 137°9′W) is in the form of a long narrow trench running north–south. It is 58.9 km long, less than 2 km wide along most of its length, and has a mean depth of 33 m except at the extreme northern and southern ends and several lateral bays which are quite shallow. Little aquatic vegetation is present, the bottom consisting for the most part of boulders and glacial rubble. Eight species of fishes are known to occur in Aishihik Lake (Anon. 1974), the most abundant species recovered in gillnet catches being lake whitefish, *Coregonus clupeaformis* (Mitchill); lake trout, *Salvelinus namaycush* (Walbaum); and round whitefish, *Prosopium cylindraceum* (Pallas). Incidental in gillnet catches were Arctic grayling, *Thymallus arcticus* (Pallas); burbot, *Lota lota* (Linnaeus); longnose sucker, *Catostomus catostomus* (Forster); and northern pike, *Esox lucius* Linnaeus. Slimy sculpin, *Cottus cognatus* Richardson, also occurred in large numbers along gravel beach areas.

Stevens Lake (61°42′N, 137°31′W) at its closest point lies less than 2 km from the north end of Aishihik Lake. It is a smaller, more eutrophic lake, approximately 11 km long with a maximum depth of approximately 12 m. During the study period the lake was characterized by low water transparency and a large number of weed beds which support a large northern pike population. Only two other species of fishes were encountered in Stevens Lake during the course of this study, lake whitefish and slimy sculpin.

A total of 309 fishes of 8 species from Aishihik Lake and 74 fishes of 3 species from Stevens Lake were examined for protozoan and metazoan parasites during the period June 7–September 21, 1973 (Table 1). The majority of fishes were obtained by gillnetting and seining. Arctic grayling and northern pike were also obtained by angling.

Within Aishihik Lake, fish samples were obtained from two areas, one at the north and the other at the south end of the lake. In each of these areas and in Stevens Lake, samples were taken during early (June 7–July 21) and late (July 22–September 20) summer. When possible, 15–20 fish of each species were obtained from each sampling area during each sampling period. Because the data proved insufficient for time period or area (in Aishihik Lake) analyses, owing to sample difference in age and sex composition, data have been combined for all samples from each lake.

Fish necropsies were usually accomplished in a field laboratory within 48 h after capture. During this period the fish were either held alive in pens in the lake or were stored on ice. A few specimens were frozen or preserved in 10% formalin for later examination.

The following tissues and organs were examined

TABLE 1. Species and numbers of fishes examined from Aishihik and Stevens lakes. Numbers in parentheses indicate number of fish from which blood smears were made.

	Aishihik Lake	Stevens Lake
1[a] *Catostomus catostomus*	6(0)	—
2 *Coregonus clupeaformis*	63(33)	30(14)
3 *Cottus cognatus*	61(15)	15(3)
4 *Esox lucius*	14(4)	29(26)
5 *Lota lota*	3(2)	—
6 *Prosopium cylindraceum*	57(25)	—
7 *Salvelinus namaycush*	61(31)	—
8 *Thymallus arcticus*	44(36)	—

[a]Reference number for Table 2.

at necropsy with the aid of a stereoscopic microscope at magnifications up to 50×: skin, fins, nasal cavities, mouth, esophagus, liver, spleen, gonads, swimbladder, stomach, pyloric caeca, intestine, heart, mesenteries, eyes, central nervous system, and musculature. Brain and kidney tissue, gall bladders, and urinary bladders were preserved in 10% formalin for later examination for protozoan (including myxosporidan) parasites. Blood samples were taken from the caudal artery by severing the caudal peduncle. Thin blood smears were prepared in the field, fixed with absolute methanol, and stained with Giemsa's stain.

Gills of fishes infected with large numbers of monogeneans were placed in a 1:4000 formalin solution for 30 min to relax the parasites. Estimation of numbers of *Tetraonchus monenteron* from *E. lucius* was accomplished by dilution of the parasite sample to a known volume (1 liter), followed by vigorous shaking to obtain uniform parasite dispersion and the removal and tabulation of parasites from two 5-ml samples.

Intestinal contents were scraped into a 1-liter glass cylinder to which was added approximately 20 g sodium bicarbonate to free the intestinal helminths from mucus. This process was repeated several times, as required, the parasites being allowed to settle to the bottom and the mucus and intestinal debris being decanted. Due to the large number of parasites found in the intestines of most fish necropsied, only representative samples of approximately 30 specimens of each type of parasite enumerated were preserved from each host. Later examination in some cases showed that samples consisted of two or more similar species which were not distinguished when collected (e.g. *Crepidostomum* spp., *Triaenophorus* spp., *Neoechinorhynchus* spp.). As a result, prevalence and intensity of infection are in some cases unavailable for individual species.

Standard techniques were used for preparing specimens for microscopic examination. Measurements were made with the aid of an ocular micrometer. Representative collections of the parasite species encountered are maintained in the Parasite Collection of the Pacific Biological Station.

Results

Forty-four species of parasites were found in fishes of Aishihik Lake and 23 in fishes from Stevens Lake (Table 2). In separate lists for each lake, the following data are reported by host for each parasite recovered: number fish infected per number fish examined, range in intensity in infected fish, mean number of parasites per infected fish ± SE, and site of infection. For example, for *Anonchohaptor anomalus* from *Catostomus catostomus*, "(5/6, 1–14, 5.8 ± 1.0) gills" indicates 5 of 6 hosts were infected with this parasite, the numbers of *A. anomalus* per infected fish ranged from 1 to 14, the mean number per infected fish was 5.8 ± 1.0 SE, and the site of infection was the gills.

Parasites of Aishihik Lake Fishes

Catostomus catostomus (Forster) (longnose sucker)
- *Myxosoma* sp. (6/6, –,–) gills
- *Anonchohaptor anomalus* (5/6, 1–14, 5.8 ± 1.0) gills
- *Diplostomum spathaceum* (metacercaria) (5/6, 2–21, 7.0 ± 1.6) vitreous humor and lens
- *Glaridacris catostomi* (5/6, 1–5, 3.0 ± 0.3) intestine
- *Cystidicola farionis* (immature) (1/6, 1, 1.0 ± 0.0) swimbladder

Coregonus clupeaformis (Mitchill) (lake whitefish)
- *Chloromyxum* sp. (7/58, –,–) gall bladder
- *Myxobolus neurobius* (53/60, –,–) brain, spinal cord
- *Henneguya zschokkei* (4/63, 1–2, 1.3 ± 0.1) musculature, pelvic fin
- *Hexamita salmonis* (6/63, –,–) gall bladder
- *Haemogregarina irkalukpiki* (4/33, –,–) erythrocytes
- *Discocotyle sagittata* (50/63, 1–43, 7.2 ± 0.2) gills
- *Crepidostomum farionis* and *C. metoecus* (27/63, 1–547, 65.8 ± 4.7) intestine, pyloric caeca
- *Diplostomum spathaceum* (metacercaria) (61/63, 4–522, 120.6 ± 2.0) vitreous humor and lens
- *Tetracotyle* sp. (metacercaria) (53/63, –,–) pericardium, surface of heart
- *Cyathocephalus truncatus* (22/63, 1–34, 7.2 ± 0.4) pyloric caeca
- *Eubothrium salvelini* (8/63, 12.7, 3.1 ± 0.6) pyloric caeca
- *Proteocephalus tumidocollus* (51/63, 1–413, 75.0 ± 2.0) pyloric caeca, intestine
- *Triaenophorus crassus* (plerocercoid) (61/63, 1–49, 15.1 ± 0.2) musculature
- *Diphyllobothrium* sp. (plerocercoid) (30/63, 1–11, 2.5 ± 0.1) encysted on digestive tract, in liver, mesenteries
- *Neoechinorhynchus tumidus* (60/63, 1–222, 47.0 ± 0.8) intestine
- *Cystidicola farionis* (48/63, 1–1136, 69.4 ± 3.5) swimbladder
- *Raphidascaris acus* (larva) (6/63, –,–) encysted on digestive tract, in liver and spleen
- *Salmincola extensus* (3/63, 1, 1.0 ± 0.0) pelvic and pectoral fins
- *Piscicola milneri* (1/63, 1, 1.0 ± 0.0) gill cavity

Cottus cognatus Richardson (slimy sculpin)
- *Myxobolus* sp. (1/61, –,–) cyst on stomach

TABLE 2. Comparison of the parasite fauna of fishes in Aishihik and Stevens lakes.

Parasite	Aishihik Lake	Stevens Lake
Protozoa		
Chloromyxum dubium Auerbach, 1908	5[a]	—
Chloromyxum esocinum Dogiel, 1934	—	4
Chloromyxum sp.	2, 8	2
Epistylis sp.	3	—
Haemogregarina irkalukpiki Laird, 1961	2, 6	2
Henneguya zschokkei (Gurley, 1893)	2, 6	—
Hexamita salmonis (Moore, 1923)	2, 5, 6, 7, 8	—
Myxidium lieberkuehni Bütschli, 1882	4	4
Myxobolus neurobius Schuberg and Schröder, 1905	2, 6, 7, 8	2
Myxobolus sp.	3	—
Myxosoma sp.	1	—
Myxobilatus yukonensis Arthur and Margolis, 1975	3	—
Sphaerospora cristata Shulman, 1962	5	—
Trichodina sp.	3	—
Monogenea		
Anonchohaptor anomalus Mueller, 1938	1	—
Dactylogyrus buddi Dechtiar, 1974	3	3
Discocotyle sagittata (Leuckart, 1842)	2, 6, 7, 8	—
Gyrodactylus bairdi Wood and Mizelle, 1957	3	—
Tetraonchus borealis (Olsson, 1893)	8	—
Tetraonchus monenteron (Wagener, 1857)	4	4
Tetraonchus variabilis Mizelle and Webb, 1953	6	—
Digenea		
Allocreadium isoporum (Looss, 1894)	4, 8	4
Crepidostomum farionis (O. F. Müller, 1784)	2, 6, 7, 8	2
Crepidostomum metoecus Braun, 1900	2, 3, 4, 5, 7, 8	2, 3, 4
Diplostomum spathaceum (Rudolphi, 1819) (metacercaria)	1, 2, 3, 4, 5, 6, 7, 8	2, 3
Heterophyidae (metacercaria)	3	—
Neascus sp. (metacercaria)	3	3
Tetracotyle sp. (metacercaria)	2, 5, 6, 7, 8	2
Cestoda		
Cyathocephalus truncatus (Pallas, 1781)	2, 6, 7	2
Diphyllobothrium sp. (plerocercoid)	2, 5, 6, 7, 8	2
Eubothrium salvelini (Schrank, 1790)	2, 6, 7, 8	2
Glaridacris catostomi Cooper, 1920	1	—
Proteocephalus tumidocollus Wagner, 1953	2, 3[b], 4[b], 6, 7, 8	2
Schistocephalus solidus (O. F. Müller, 1780) (plerocercoid)	3	—
Triaenophorus crassus Forel, 1768		
adult	4	4
plerocercoid	2, 6, 7, 8	2
Triaenophorus nodulosus (Pallas, 1781)		
adult	—	4
plerocercoid	—	3
Acanthocephala		
Neoechinorhynchus rutili (O. F. Müller, 1780)	3[b], 4[b], 5, 7, 8	—
Neoechinorhynchus tumidus Van Cleave and Bangham, 1949	2, 3[b], 4[b], 6, 8	2, 4[b]
Nematoda		
Capillaria salvelini Polyansky, 1952	6, 7, 8	—
Cystidicola farionis Fischer, 1798	1[b], 2, 6, 7, 8	2
Haplonema hamulatum Moulton, 1931	5	—
Raphidascaris acus (Bloch, 1779)		
adult	4	4
larvae	2, 8	2, 3, 4
Copepoda		
Salmincola edwardsii (Olsson, 1869)	7	—
Salmincola extensus (Kessler, 1868)	2	—
Salmincola thymalli (Kessler, 1868)	8	—
Hirudinoidea		
Piscicola milneri (Verrill, 1874)	2, 4, 5, 6, 7	2, 4

[a]Indicates host reference number in Table 1.
[b]Indicates hosts from which only immature parasites were recovered.

Myxobilatus yukonensis (2/52, –,–) kidney tubules, urinary bladder
Trichodina sp. (14/61, –,–) gills
Epistylis sp. (5/61, –,–) fins
Dactylogyrus buddi and *Gyrodactylus bairdi* (58/61, 1–43, 12.1 ± 0.2) gills, external body surface
Crepidostomum metoecus (19/61, 1–6, 1.5 ± 0.1) intestine
Diplostomum spathaceum (metacercaria) (60/61, 4–6100, 1054.2 ± 21.8) vitreous humor
Heterophyidae (metacercaria) (2/61, 2, 2.0 ± 0.0) encysted on gills
Neascus sp. (metacercaria) (56/61, –,–) free and encysted on peritoneum, in musculature
Proteocephalus tumidocollus (immature) (12/61, 1–7, 2.5 ± 0.2) pyloric caeca, intestine
Schistocephalus solidus (plerocercoid) (5/61, 1, 1.0 ± 0.0) body cavity
Neoechinorhynchus tumidus (immature) and *N. rutili* (immature) (21/61, 1–13, 2.1 ± 0.1) intestine

Esox lucius Linnaeus (northern pike)
Myxidium lieberkuehni (5/9, –,–) urinary bladder
Tetraonchus monenteron (14/14, 120–4400, 879.6 ± 76.0) gills
Allocreadium isoporum (1/14, 1, 1.0 ± 0.0) intestine
Crepidostomum metoecus (1/14, 1, 1.0 ± 0.0) intestine
Diplostomum spathaceum (metacercaria) (1/14, 1, 1.0 ± 0.0) vitreous humor
Proteocephalus tumidocollus (immature) (4/14, 1–4, 2.3 ± 0.4) intestine
Triaenophorus crassus (9/14, 2–80, 24.7 ± 7.2) intestine
Neoechinorhynchus tumidus (immature) and *N. rutili* (immature) (1/14, 7, 7.0 ± 0.0) intestine
Raphidascaris acus (adult) (8/14, 1–12, 4.1 ± 0.8) intestine
Piscicola milneri (1/14, 1, 1.0 ± 0.0) fins, external body surface

Lota lota (Linnaeus) (burbot)
Chloromyxum dubium (2/3, –,–) gall bladder
Sphaerospora cristata (3/3, –,–) urinary bladder
Hexamita salmonis (2/3, –,–) gall bladder
Crepidostomum metoecus (2/3, 6–11, 8.5 ± 1.8) intestine
Diplostomum spathaceum (metacercaria) (2/3, 63–157, 110.0 ± 33.2) vitreous humor and lens
Tetracotyle sp. (metacercaria) (1/3, –,–) surface of heart
Diphyllobothrium sp. (plerocercoid) (1/3, 1, 1.0 ± 0.0) encysted on digestive tract
Neoechinorhynchus rutili (1/3, 1, 1.0 ± 0.0) intestine
Haplonema hamulatum (2/3, 1–17, 9.0 ± 5.6) intestine
Piscicola milneri (1/3, 1, 1.0 ± 0.0) external body surface

Prosopium cylindraceum (Pallas) (round whitefish)
Myxobolus neurobius (37/41, –,–) brain, spinal cord
Henneguya zschokkei (30/57, 1–40, 7.4 ± 0.3) caudal musculature
Hexamita salmonis (3/52, –,–) gall bladder
Haemogregarina irkalukpiki (1/25, –,–) erythrocytes
Discocotyle sagittata (32/57, 1–29, 6.8 ± 0.3) gills
Tetraonchus variabilis (31/57, 1–148, 20.5 ± 0.9) gills
Crepidostomum farionis (49/57, 1–42, 6.4 ± 1.0) intestine
Diplostomum spathaceum (metacercaria) (54/57, 1–44, 6.6 ± 0.2) vitreous humor and lens
Tetracotyle sp. (metacercaria) (42/57, –,–) pericardium, surface of heart
Cyathocephalus truncatus (1/57, 2, 2.0 ± 0.0) pyloric caeca
Eubothrium salvelini (2/57, 1–25, 13.0 ± 8.5) pyloric caeca
Proteocephalus tumidocollus (15/57, 1–40, 4.7 ± 0.7) pyloric caeca, intestine
Triaenophorus crassus (plerocercoid) (3/57, 1–3, 1.7 ± 0.4) musculature
Diphyllobothrium sp. (plerocercoid) (3/57, 1–6, 3.0 ± 0.1) encysted on digestive tract, in liver and mesenteries
Neoechinorhynchus tumidus (49/57, 1–26, 5.1 ± 0.1) intestine
Cystidicola farionis (24/57, 1–14, 4.0 ± 0.2) swimbladder
Capillaria salvelini (1/57, 1, 1.0 ± 0.0) intestine
Piscicola milneri (2/57, 2, 2.0 ± 0.0) pectoral fins

Salvelinus namaycush (Walbaum) (lake trout)
Myxobolus neurobius (61/61, –,–) brain, spinal cord
Hexamita salmonis (29/60, –,–) gall bladder
Discocotyle sagittata (1/61, 5, 5.0 ± 0.0) gills
Crepidostomum farionis and *C. metoecus* (55/61, 1–596, 62.6 ± 2.2) intestine
Diplostomum spathaceum (metacercaria) (61/

61, 6–857, 143.2 ± 2.7) vitreous humor and lens
Tetracotyle sp. (metacercaria) (49/61, –,–) pericardium, surface of heart
Cyathocephalus truncatus (13/61, 1–48, 16.2 ± 1.8) pyloric caeca
Eubothrium salvelini (58/61, 1–315, 35.8 ± 0.9) pyloric caeca
Proteocephalus tumidocollus (61/61, 2–2855, 325.9 ± 10.0) pyloric caeca, intestine
Triaenophorus crassus (plerocercoid) (14/61, 1–6, 2.1 ± 0.1) musculature
Diphyllobothrium sp. (plerocercoid) (27/61, 1–9, 2.6 ± 0.1) encysted on digestive tract, in liver and mesenteries
Neoechinorhynchus rutili (31/61, 1–57, 14.8 ± 0.4) intestine
Cystidicola farionis (50/61, 1–387, 62.3 ± 2.1) swimbladder
Capillaria salvelini (13/61, 1–20, 3.7 ± 0.4) intestine
Salmincola edwardsii (27/61, 1–9, 1.9 ± 0.1) fins, gills, external body surface
Piscicola milneri (4/61, 1–3, 1.8 ± 0.2) fins, external body surface

Thymallus arcticus (Pallas) (Arctic grayling)
Chloromyxum sp. (2/40, –,–) gall bladder
Myxobolus neurobius (34/40, –,–) brain, spinal cord
Hexamita salmonis (30/40, –,–) gall bladder
Discocotyle sagittata (9/44, 1–34, 6.2 ± 1.2) gills
Tetraonchus borealis (39/44, 1–70, 8.9 ± 0.3) gills
Allocreadium isoporum, *Crepidostomum farionis*, and *C. metoecus* (42/44, 1–154, 31.2 ± 0.9) intestine
Diplostomum spathaceum (metacercaria) (38/44, 2–1862, 132.1 ± 10.7) vitreous humor and lens
Tetracotyle sp. (metacercaria) (6/44, –,–) pericardium, surface of heart
Eubothrium salvelini (7/44, 1–7, 3.1 ± 0.3) pyloric caeca
Proteocephalus tumidocollus (12/44, 1–26, 6.7 ± 0.7) pyloric caeca, intestine
Triaenophorus crassus (plerocercoid) (18/44, 1–11, 3.4 ± 0.2) musculature
Diphyllobothrium sp. (plerocercoid) (8/44, 1–16, 3.1 ± 0.7) encysted on digestive tract, in liver
Neoechinorhynchus rutili and *N. tumidus* (8/44, 1–3, 1.6 ± 0.1) intestine
Cystidicola farionis (5/44, 1–2, 1.4 ± 0.1) swimbladder
Capillaria salvelini (1/44, 2, 2.0 ± 0.0) intestine
Raphidascaris acus (larva) (8/44, 1–9, 4.0 ± 0.4) encysted in liver
Salmincola thymalli (15/44, 1–46, 6.3 ± 1.0) gills

Parasites of Stevens Lake Fishes

Coregonus clupeaformis (lake whitefish)
Chloromyxum sp. (2/29, –,–) gall bladder
Myxobolus neurobius (30/30, –,–) brain, spinal cord
Haemogregarina irkalukpiki (3/14, –,–) erythrocytes
Crepidostomum farionis and *C. metoecus* (17/30, 1–256, 52.2 ± 4.7) intestine
Diplostomum spathaceum (metacercaria) (29/30, 17–1074, 199.0 ± 8.8) vitreous humor and lens
Tetracotyle sp. (metacercaria) (24/30, –,–) pericardium, surface of heart
Cyathocephalus truncatus (4/30, 1–13, 4.5 ± 1.4) pyloric caeca
Eubothrium salvelini (10/30, 1–2, 1.4 ± 0.0) pyloric caeca
Proteocephalus tumidocollus (25/30, 1–632, 59.0 ± 6.2) pyloric caeca, intestine
Triaenophorus crassus (plerocercoid) (26/30, 1–71, 21.3 ± 0.8) musculature
Diphyllobothrium sp. (plerocercoid) (7/30, 1–2, 1.4 ± 0.1) encysted on digestive tract, in liver
Neoechinorhynchus tumidus (17/30, 1–30, 5.6 ± 0.5) intestine
Cystidicola farionis (26/30, 1–147, 25.2 ± 1.3) swimbladder
Raphidascaris acus (larva) (30/30, –,–) intestinal wall, liver, spleen
Piscicola milneri (1/30, 1, 1.0 ± 0.0) external body surface

Cottus cognatus (slimy sculpin)
Dactylogyrus buddi (4/15, 1–3, 1.5 ± 0.2) gills
Crepidostomum metoecus (10/15, 1–13, 4.6 ± 0.4) intestine
Diplostomum spathaceum (metacercaria) (5/15, 1–104, 34.4 ± 8.9) vitreous humor
Neascus sp. (metacercaria) (14/15, –,–) free and encysted on peritoneum, in musculature
Triaenophorus nodulosus (plerocercoid) (1/15, 1, 1.0 ± 0.0) encysted on stomach
Raphidascaris acus (larva) (1/15, 1, 1.0 ± 0.0) encysted on stomach

Esox lucius (northern pike)
Chloromyxum esocinum (11/29, –,–) gall bladder
Myxidium lieberkuehni (11/23, –,–) urinary bladder

TABLE 3. Comparison of *Tetraonchus borealis* (Olsson, 1893) and *T. rauschi* Mizelle and Webb, 1953 (measurements in millimeters).

	T. rauschi[a]	*T. borealis*[b]	*T. borealis* (10 specimens)[c]
Length	1.19 –2.52	1.2 –2.1	1.01 –1.78
Width	0.198–0.288	0.18 –0.30	0.20 –0.50
Cirrus length	0.082–0.112	0.072–0.095	0.091–0.117
Accessory piece length	0.077–0.118	0.070–0.090	0.086–0.118
Ventral bar length	0.05 –0.072	0.056–0.078	0.068–0.105
Dorsal anchor length	0.093–0.139	0.082–0.106	0.082–0.107
Ventral anchor length	0.101–0.135	0.077–0.125	0.093–0.120
Marginal hook length	0.014	0.012–0.015	0.012–0.015
Hosts	*Thymallus arcticus*	*T. arcticus* *T. thymallus*	*T. arcticus*
Localities	Alaska	Far-eastern USSR Mongolia	Yukon Territory

[a]Measurements from Mizelle and Webb (1953).
[b]Measurements from Bykhovskaya-Pavlovskaya et al. (1962) and Ergens and Lom (1970).
[c]Original data.

Tetraonchus monenteron (26/29, 1–2030, 495.7 ± 24.8) gills
Allocreadium isoporum and *Crepidostomum metoecus* (9/29, 2–690, 197.0 ± 28.9) intestine
Triaenophorus crassus and *T. nodulosus* (27/29, 1–237, 81.3 ± 2.6) intestine
Neoechinorhynchus tumidus (immature) (4/29, 1–3, 1.5 ± 0.3) intestine
Raphidascaris acus (adult) (23/29, 1–95, 20.0 ± 1.0) intestine
R. acus (larva) (1/29, 1, 1.0 ± 0.0) encysted in spleen
Piscicola milneri (4/29, 1–2, 1.5 ± 0.2) fins, external body surface

Remarks on the Systematics of Certain Species

MONOGENEA

Tetraonchus borealis (Olsson, 1893) (syn.: *T. rauschi* Mizelle and Webb, 1953) — Mizelle and Webb (1953) described *T. rauschi* from the gills of *Thymallus signifer* (syn. of *T. arcticus*) from Alaska. The description of their material, which apparently was compared only with species of *Tetraonchus* reported from North American fishes, corresponds with that of *T. borealis* as given by Bykhovskaya-Pavlovskaya et al. (1962), Ergens and Lom (1970), and Ergens (1971). Of utmost importance in the taxonomy of this genus is the structure and relationship of the cirrus and accessory piece, and the structure of the anchors and connecting bar. The morphology of these structures is identical in both species and the accessory piece forms 1–1¼ turns about the cirrus. On this basis and on the basis of comparative morphological and host data summarized in Table 3, *T. rauschi* is considered a synonym of *T. borealis.*

NEMATODA

Cystidicola farionis (Fischer, 1798) (syn.: *C. stigmatura* (Leidy, 1886)) — Ko and Anderson (1969), in their revision of the genus *Cystidicola*, found that specimens of the nearctic *C. stigmatura* were morphologically indistinguishable from the palearctic *C. farionis.* However, they refrained from synonymizing *C. stigmatura* with *C. farionis* prior to obtaining supporting evidence from life cycle studies. Other authors (Campana-Rouget 1955; Moravec and Ergens 1970) have also suggested that *C. stigmatura* is probably a synonym of *C. farionis.* We believe there is no longer justification for retaining *C. stigmatura* as an independent species and consider it to be a synonym of *C. farionis.*

Raphidascaris acus (Bloch, 1779) (syn.: *R. canadensis* Smedley, 1933) — Smedley (1933) described *R. canadensis* from the intestine of *Esox lucius* from various localities in Manitoba and Saskatchewan. Her description was extremely brief and no comparisons with existing members of the genus were presented. In addition to our Yukon material we have examined specimens collected from *E. lucius* from Montreal Lake, Saskatchewan, in 1955 and have found them to be morphologically identical with *R. acus* as described by Moravec (1971) from *E. lucius* from Czechoslovakia (Table 4). The description by Smedley (1933) of subequal spicules and lateral alae of unequal breadth is unsupported by our examination of the above nearctic material.

TABLE 4. Comparison of *Raphidascaris acus* (Bloch, 1779) and *R. canadensis* Smedley, 1933 (measurements in millimeters).

		R. canadensis[a]	*R. acus* original (Saskatchewan)	*R. acus* original (Yukon)	*R. acus*[b]
Length	♂	23.0 (max.)	28.5 –29.4	17.0 –35.5	12.24 –37.76
	♀	50.0 (max.)	36.3 –47.2	18.0 –47.3	20.53 –43.86
Maximum width	♂	—	0.62– 0.77	0.32– 0.59	0.340– 1.557[c]
	♀	—	0.78– 1.14	0.40– 0.85	0.47 – 0.88
Esophagus length	♂	⅛ total length	2.46– 2.92	1.93– 3.34	1.92 – 3.80
	♀		3.25– 3.86	2.10– 5.10	2.51 – 3.17
Appendix length	♂	—	0.89– 2.34	0.76– 1.90	1.01 – 2.11
	♀	—	1.73– 1.76	0.60– 2.32	0.856– 1.591
Tail length	♂	—	0.21– 0.27	0.14– 0.22	0.108– 0.231
	♀	0.55	0.58– 0.64	0.32– 0.56	0.258– 0.490
Distance of vulva to anterior end		⅛ total length	⅛ total length	⅓–¼ total length	Located in anterior half of body
Spicule length		0.65 subequal	0.74–0.77 equal	0.55–0.86 equal	0.705–1.053 equal
No. pairs caudal papillae		About 21	19–20 preanal, 5 postanal (1st pair double and sometimes separated) and unpaired medial papilla-like formation on anterior cloacal lip	18–20 preanal, 5 postanal (1st pair double and sometimes separated) and unpaired medial papilla-like formation on anterior cloacal lip	17–20 preanal, 5 postanal (1st pair double and sometimes separated) and unpaired papilla-like formation on anterior cloacal lip
Host		*Esox lucius*	*E. lucius*	*E. lucius*	*E. lucius* (and others)
Localities		Manitoba and Saskatchewan (various lakes)	Montreal Lake, Saskatchewan	Aishihik and Stevens lakes, Yukon Territory	Czechoslovakia (various localities)

[a]Measurements from Smedley (1933).
[b]Measurements from Moravec (1971).
[c]Range given is probably erroneous and likely should read 0.340–0.557.

Davies (1967) suggested that no valid reasons existed to differentiate these two species on the basis of published descriptions and on similar life cycles as indicated by her own studies and that of Thomas (1937). We consider *R. canadensis* a synonym of *R. acus*.

Capillaria salvelini Polyansky, 1952 — *Capillaria salvelini* is extremely similar to *C. coregoni* Shulman-Albova, 1953, a parasite of coregonine fishes of the USSR. Because of slight differences between Aishihik Lake specimens of *C. salvelini* and published descriptions of these two species (see Polyansky 1952; Threlfall and Hanek 1969; Shulman-Albova 1953; Belous 1965), an attempt was made to obtain previously identified material for comparison. The original specimens of *C. salvelini* and *C. coregoni* apparently are no longer extant (R. Shulman personal communication). We have examined specimens of *C. salvelini* provided by Dr J. H. C. Pippy from smolts of *Salmo salar* Linnaeus collected during 1966 from Deadmans Bay River, Newfoundland; Saint John River and Miramichi River, New Brunswick; North Esk River, Scotland; Burrishode River, Ireland; and Coquet River, England; as well as specimens provided by Dr G. Hanek from St. Johns, Nfld. Attempts to obtain specimens of *C. coregoni* were unsuccessful. Based on published descriptions, the only difference between *C. salvelini* and *C. coregoni* lies in the eggs, those of *C. coregoni* being embryonated and possessing protruding polar plugs whereas those of *C. salvelini* are unembryonated and lack protruding polar plugs. Eggs of all specimens of *C. salvelini* examined during this study were unembryonated and possessed protruding polar plugs. In addition, both original descriptions note the presence of an elastic coiled thread around the base of the spicule in these two species. Belous (1965) did not detect such a thread in his material of *C. coregoni* and likewise we have been unable to detect this structure in *C. salvelini*. However, we have noted what appears to be a wrinkling of the spicule sheath in several specimens of *C. salvelini* and believe that this may have been mistaken for a thread by the original author. It seems likely that *C. coregoni* is a synonym of *C. salvelini* but a definitive decision must await examination and comparison of topotypic material of these two species.

Discussion

The results of this survey provided four new North American records. These are: *Chloromyxum dubium* and *Sphaerospora cristata* from *Lota lota* from Aishihik Lake; *Ch. esocinum* from *Esox lucius* from Stevens Lake; and *Crepidostomum metoecus* from *Coregonus clupeaformis*, *Cottus cognatus*, *E. lucius*, *L. lota*, *Salvelinus namaycush*, and *Thymallus arcticus* from Aishihik Lake and *Coregonus clupeaformis*, *Cottus cognatus*, and *E. lucius* from Stevens Lake. In addition, the finding of the two monogeneans *Dactylogyrus buddi* and *Gyrodactylus bairdi* on *C. cognatus* extends their distribution from the Great Lakes region far to the northwest in North America.

The four new North American records of

species previously known from the palearctic and the synonymizing of several nearctic species with previously described palearctic species reinforces the similarity of the parasite fauna of the fishes of these two regions as has been discussed recently by Bauer and Gusev (1969). More extensive investigation of the parasite fauna of nearctic fishes will likely show many other species to be holarctic in distribution.

Although the present study appears to be the first to examine the potential parasitological consequences of connecting two water bodies, Lindsey (1957) speculated on the possible effects of a number of proposed water diversions in British Columbia and cautioned that the pathogenic cestode *Triaenophorus crassus* Forel, 1868 might be introduced and become established in new areas by movement of its definitive host, *E. lucius*. There exist numerous reports of transfers of fish parasites from other types of human activities, primarily the transfer of fish between water bodies, often with serious consequences. This literature has recently been summarized by Hoffman (1970).

As is often the case with environmental impact studies such as that conducted for the Aishihik Lake hydroelectric development, decisions that may have long range and often irreversible environmental effects must be based on information that, due to the need for immediate answers and limitations in manpower, is less conclusive than might be desired. Although comparisons and conclusions drawn in this study are limited by such factors as nonrandom sampling, small sample size, and variation in age and sex composition between samples, useful qualitative comparisons can be made between the two lakes and possible implications of the introduction of potentially harmful parasite species examined.

Comparison of the parasite fauna found in fishes of Aishihik Lake with that of fishes of Stevens Lake indicated that of the 44 species recovered from 8 species of fishes in Aishihik Lake, 23 were not found in Stevens Lake (Table 2). Of the 23 species of parasites recovered from the 3 species of fishes occurring in Stevens Lake only 2 were not found in Aishihik Lake. Known pathogenic species found in only one of the lakes studied are *Henneguya zschokkei*, *Hexamita salmonis*, *Discocotyle sagittata*, and *Neoechinorhynchus rutili* from Aishihik Lake, and *Triaenophorus nodulosus* from Stevens Lake.

The proposed plan for the diversion of water between the two lakes called for the total diversion of flow from Stevens Lake into Aishihik Lake through the blockage of its present outlet into the Yukon River system. Thus any potentially harmful parasites entering into this drainage system from Aishihik Lake would contaminate only Stevens Lake. Of the potential pathogens that may become established in Stevens Lake, *Henneguya zschokkei*, *Hexamita salmonis*, and *Discocotyle sagittata* require no intermediate hosts, while *Neoechinorhynchus rutili* utilizes ostracods (Walkey 1962; Merritt and Pratt 1964) which are likely to be already present in Stevens Lake. Thus, it is probable that any of the above parasites would become established should they be introduced into Stevens Lake.

Of particular concern is *Discocotyle sagittata* which infects the gills of all species of salmonids present in Aishihik Lake. Heavy infections were observed to produce anemia and associated weakness in *Coregonus clupeaformis*; a fish infected with approximately 200 flukes had a hematocrit of only 4% as opposed to approximately 40% in lightly infected individuals.

Of an even more serious nature is the potential introduction of pathogenic species of parasites into the Alsek River system from Stevens Lake, since, due to the position of Aishihik Lake at the headwaters of its drainage system, the potential exists not only for the contamination of Aishihik Lake but of all waters in the Alsek River system below the lake.

Thus it is likely that unless preventive measures were to be taken the pathogenic cestode *Triaenophorus nodulosus* would be introduced into the Alsek River system and would probably become established in Aishihik Lake since suitable definitive and intermediate hosts are known to be present there. The pathogenesis of the plerocercoid of *T. nodulosus* in the second intermediate host is well known (Miller 1945; Petrushevsky and Shulman 1958; Bauer 1959). Site of infection is most commonly the liver, where damage caused by parasite penetration often results in liver inflammation and death, particularly in young fish. Although the actual consequences resulting from the introduction of this parasite cannot be predicted, it could represent a serious threat to the substantial populations of salmonids occurring in Aishihik Lake and possibly elsewhere in the Alsek drainage.

Effects of the other parasites apparently confined to one of the investigated lakes are unknown, but it is generally recognized that the introduction of normally nonpathogenic parasites into a population of previously unexposed hosts may result in highly pathogenic infections. However, many species of parasites may not be able to become established in new areas due to unsuitable environmental conditions or the absence of required intermediate hosts.

It is apparent from the substantial differences observed in the parasite fauna of Aishihik and Stevens lakes that any proposal for the construction of a diversion canal must consider means for preventing the transfer of potential fish pathogens. Factors that must be given attention include preventing the transfer of infected fishes, infected intermediate hosts, free-swimming larval stages, and contaminated host waste products. In the case under consideration, if the flow of water is of continuous duration and sufficient volume, movement of free-swimming larval forms and contaminated wastes from Aishihik into Stevens Lake would not take place. Movement of fishes and those invertebrate intermediate hosts that are capable of movement against current would, however, have to be prevented, perhaps through the use of mechanical and electrical barriers.

Preventing the establishment of *T. nodulosus* in Aishihik Lake would require either the eradication of the parasite from Stevens Lake or, if feasible, the construction of physical and electrical barriers that would not only prevent movement of the fish between the two lakes, but would also destroy all free-living parasite larval stages and infected invertebrate intermediate hosts which pass through the diversion canal.

The considerable research effort expended on attempts to control *Triaenophorus crassus* in central Canadian lakes (a serious problem to the commercial whitefish industry) indicates that the total eradication of *T. nodulosus* from Stevens Lake through existing methods would prove restrictively expensive and given the lake's relatively large area (approximately 15 km^2) would probably be unsuccessful (Miller 1952; Doan 1953; Lawler 1959, 1965).

Although the water diversion discussed here has for the present been abandoned for reasons unrelated to possible parasite transfer, the rapid development of the Canadian north combined with the increasing demand for electrical power will undoubtedly result in plans for similar water diversions in the future. This study indicates that the introduction of parasites of economic and pathogenic importance as a result of such activities must be considered a threat, and extensive investigation of the parasite fauna of fishes in areas to be connected should be undertaken, followed by implementation of measures to prevent transfaunation of parasites, before such water diversions are authorized.

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Taxonomic Reevaluation of the Spiny Dogfish (*Squalus acanthias* L.) in the Northeastern Pacific Ocean

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JONES, B. C., AND G. H. GEEN. 1976. Taxonomic reevaluation of the spiny dogfish (*Squalus acanthias* L.) in the northeastern Pacific Ocean. J. Fish. Res. Board Can. 33: 2500–2506.

Morphometric ratios, vertebral counts, and electrophoretic analyses of spiny dogfish from east and west coasts of North America indicate that those in the northeastern Pacific Ocean comprise one of several discontinuous stocks of the cosmopolitan species *Squalus acanthias* L. Though the individual stocks exhibit statistically significant differences in meristic and biochemical characteristics, available data do not support subspecific status for any of the groups around the Americas. The inadequacy of certain morphometric data to distinguish between *Squalus* species is also discussed.

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Les rapports morphométriques, comptages vertébraux et analyses électrophorétiques de l'aiguillat commun des côtes orientale et occidentale de l'Amérique du Nord démontrent que ceux qui habitent la partie nord-est du Pacifique sont un parmi plusieurs stocks discontinus de l'espèce cosmopolite, *Squalus acanthias* L. Bien que les stocks individuels montrent des différences significatives à l'analyse statistique dans leurs caractères numériques et biochimiques, les données disponibles ne permettent pas d'accorder le statut de sous-espèce à aucun des groupes qui se trouvent autour des Amériques.

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THE spiny dogfish type specimen, designated as *Squalus acanthias* by Linnaeus, was described from European waters in 1758. Various stocks of morphologically similar animals in different parts of the world have since been referred to by this name, although sometimes divided as subspecies or different species altogether. Several authors (Bigelow and Schroeder 1948; Kato et al. 1967; Hart 1973) consider the northeastern Pacific stock, normally inhabiting continental shelf regions ranging from Baja California to the southern Bering Sea (Springer and Garrick 1964; Hart 1973), as belonging to this cosmopolitan species, but further propose that it be accorded subspecific rank based on differences in morphometric ratios and vertebral numbers.

According to Mayr (1969), "a subspecies is an aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of a species, and differing taxonomically from other populations of the species." Within this definition subspecies are required to differ significantly in one or more morphological characters. To clarify the taxonomic status of spiny dogfish in this area both from the species and subspecies points of view, we present data on morphometric ratios, vertebral counts, and electrophoretic characteristics from samples collected on east and west coasts of North America. These are compared with results of other workers on various stocks within the genus *Squalus* around the world.

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Materials and Methods

Spiny dogfish used in this study were collected during 1973–74 on the west coast of North America, primarily from the Strait of Georgia, British Columbia. Other dogfish, predominantly larger individuals, were taken from Queen Charlotte Sound, B.C., and in Alaska, California, Newfoundland, and Nova Scotia waters.

MORPHOMETRIC RATIOS

Strait of Georgia data were obtained from 182 individuals encompassing the full size range. Data were collected to permit calculation of two morphometric ratios. The first ratio (as used by previous authors) involves comparison of the length (F) of the pectoral fin measured from its origin at the fifth gill slit to its tip with head length (H) as measured between the fifth gill slit and the center of the nares

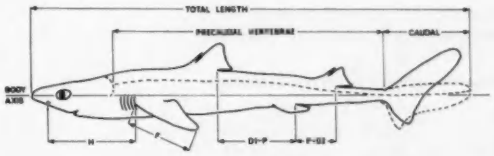

FIG. 1. *Squalus acanthias* indicating the morphometric measurements used in this study (defined more fully in text).

(Fig. 1). The second ratio is the length (P-D2), in line with the body axis, from the rear base of the pelvic fin (P) to the rear base of the second dorsal fin (D2) compared with the length (D1-P) from P to the rear base of the first dorsal fin (D1). These ratios are related to total body length (tip of snout to tip of caudal fin when depressed to align with body axis) following the method of Lindberg and Legeza (1956) and Forrester (1972).

VERTEBRAL COUNTS

The number of vertebrae from 7 male (length 27–89 cm) and 10 female dogfish (27–109 cm) collected from the Strait of Georgia were counted from X-ray negatives. Prior to x-raying a pin was placed at right angles to the body axis through the precaudal pit (Fig. 1), a depression at the dorsal base of the caudal fin, to permit identification of precaudal and caudal vertebrae (Springer and Garrick 1964). Dogfish were x-rayed using the method and equipment described by Turner (1965), but for better resolution vertebral columns were partially stripped of flesh and placed over Kodak RP Royal 2 film at a distance of 1 m from a General Electric 15-90 X-ray unit.

ELECTROPHORETIC ANALYSES

Three or four adult dogfish of each sex from each area were frozen within 4 h of capture. Muscle and blood samples were taken for starch-gel electrophoresis from the recently thawed individuals and analyzed following Tsuyuki et al. (1965).

Results and Discussion

PECTORAL FIN–HEAD LENGTH RATIO

Lindberg and Legeza (1959) suggested that spiny dogfish on the east and west coasts of North America be called *S.a. acanthias* and *S.a. suckleyi*, respectively, based on F:H ratio differences. Our F:H ratio data for the Strait of Georgia indicate significant ($P < 0.05$) positive regressions on length for reproductively immature animals, but not for transitional (dogfish showing some sign of gonad or secondary sexual characteristic development) and mature ones. Most of our other ratio data from Alaska, California, Newfoundland, and Nova Scotia dogfish fall within the Strait of Georgia F:H data confidence limits (Fig. 2), as do those of Garrick (1960) for New Zealand dogfish, and those of Lindberg and Legeza (1956) for their short fin form from European and northwestern Pacific waters. This suggests that there is no justifiable subspecific distinction among dogfish from these areas. However, the F:H ratio of the long fin form (Lindberg and Legeza 1956), as represented by specimens from the Barents and White seas in northern USSR waters and off California, gener-

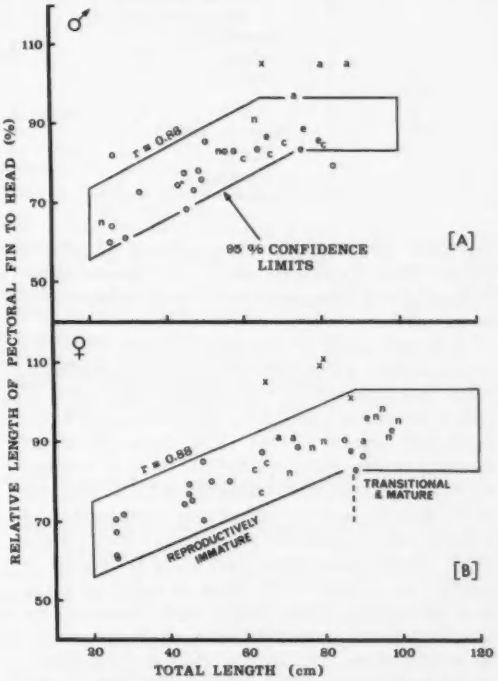

FIG. 2. Relationship of relative length of pectoral fin to head and total body length for *S. acanthias*; A) males and B) females. Enclosed areas represent the 95% confidence limits around the Strait of Georgia data (not plotted) for the length ranges sampled. Regressions for ratio on length of immature animals are $R(\%) = 54.4 + 0.506$ L (centimeters) for males and $R(\%) = 57.2 + 0.409$ L (centimeters) for females. Regressions were not significant for transitional and mature dogfish; means ±1 SD are 89.7 ± 3.4 and 92.6 ± 5.1 for males and females, respectively. Data from Lindberg and Legeza (1956) for the short fin (○) and long fin (×) forms are superimposed, as are those of Garrick (1960) for New Zealand (n) and dogfish in this study from the east coast of Canada (e), Alaska (a), and California (c).

TABLE 1. Comparison of total body length with pectoral fin length relative to head (F:H ratio) for *Squalus acanthias* from British Columbia waters.

Area, source, sex	No. sampled	Data range: Body length (*cm*)	Data range: F:H ratio (%)
Strait of Georgia			
This study			
Males (immature)	46	25.3–69.4	57.1–91.5
(trans. and mature)	27	71.8–97.8	84.4–97.2
Females (immature)	68	24.3–94.5	54.2–98.6
(trans. and mature)	32	78.3–122.5	80.6–104.3
Forrester (1972)			
Males	168	71.6–91.5	81.8–100.0
Females	33	72.6–113.5	85.2–100.0
Queen Charlotte Sound			
Forrester (1972)			
Males	51	48.0–89.8	73.9–97.8
Females	51	47.6–111.7	74.8–95.7

ally falls outside the Strait of Georgia confidence limits. The California data are questionable, being derived from one 65-cm male preserved for nearly 100 yr.

Although most of our dogfish were measured in the freshly killed state, the Alaskan specimens were first preserved in formalin, and had F:H ratios for males similar to those found by Lindberg and Legeza (1956). Two 60-cm Strait of Georgia males preserved for 10 days in isotonic 10% formalin solution exhibited a 2.1% increase in F:H ratio due to differential shrinkage, and a 5.1% length decrease (Jones and Geen 1976). Thus, shrinkage of head and body both tend to produce a greater F:H ratio. Accordingly, the long fin status of the single male described by Lindberg and Legeza (1956) is likely an artifact of preservation. The data collected from males of all stocks sampled in this and other studies should, hence, fall within the Strait of Georgia confidence limits.

The long fin data of Lindberg and Legeza (1956) of female dogfish from northern USSR waters were taken from four individuals 65–87 cm long. The F:H ratios of three fall outside our Strait of Georgia confidence limits (Fig. 2), and one of these is near the upper extremity of our range for females (Table 1). Preservation effects do not appear to account for the remaining F:H ratio differences. However, when relative fin lengths of dogfish from around the world are compared to the mean summer sea surface temperatures at their locations of capture, a negative regression is obtained ($r = -0.78$, $P < 0.001$, $n = 18$). This indicates that the F:H ratio may be environmentally influenced suggesting that there is insufficient evidence to justify subspecific distinction for the long fin forms. In addition, dogfish migrations have occurred between regions designated by Lindberg and Legeza (1959) as having the long and short fin stocks (Fig. 3). Consequent interbreeding would tend to eliminate fin differences even if this were a purely genetic character. Thus, variations in F:H ratio do not indicate the existence of differences between stocks that are not attributable to preservation artifacts or environmental modifications.

TOTAL VERTEBRAL NUMBER

The other characteristic proposed to distinguish the northeastern Pacific dogfish as a subspecies of *S. acanthias* distinct from the Atlantic form was vertebral numbers. Our data indicate that neither total length nor sex are correlated with vertebral numbers, but that numbers from east and west coasts of North America are significantly different (Table 2). However, a southeastern Pacific stock has vertebral numbers somewhat intermediate to these groups (Fig. 3). Mayr (1969) points out that if the data ranges for particular species characteristics overlap between supposedly discontinuous stocks by more than 20%, then by convention they do not deserve subspecific recognition. Overlap is 29% between the northeastern and southeastern Pacific stocks, and 21% between this latter stock and the northwestern Atlantic stock (Table 3). Thus, subspecific designation for

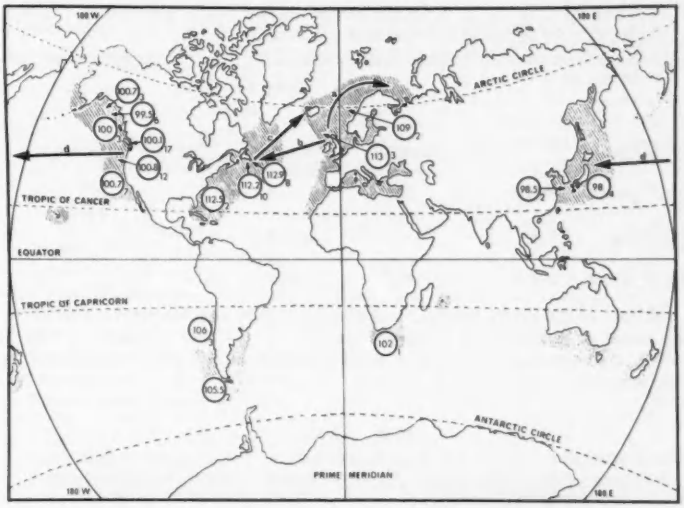

FIG. 3. Approximate global distribution of *S. acanthias* (shaded area) as derived from Bigelow and Schroeder (1957), Lindberg and Legeza (1956), Springer and Garrick (1964), and Hart (1973) showing mean total vertebral numbers (circled) and the number of dogfish sampled to lower right (from Templeman 1944; Springer and Garrick 1964; this study) for different areas. Arrows indicate apparent movements of dogfish between stocks as determined by tagging studies; a, Scotland to Barents Sea (Aasen 1962); b, Scotland to Newfoundland (Holden 1967); c, Newfoundland to Iceland (Templeman 1958); and d, Washington to Japan (Anon. 1952).

TABLE 2. Comparison of vertebral numbers of *S. acanthias* from the east and west coasts of North America.

Area	No. sampled	Mean no. vertebrae			Range of total
		Precaudal	Caudal	Total	
Alaska	6	71.5	28.0	99.5	96–104
British Columbia					
Queen Charlotte Sound	3	71.5	28.5	100.0	98–103
Strait of Georgia	17	71.0	29.1	100.1	97–103
California	7	72.6	28.1	100.7	97–109
West coast[a]	33	71.5±2.1[b]	28.6±1.0	100.1±2.7	96–109
East coast	8	82.7±1.8	30.2±1.4	112.9±2.4	109–116
Difference		11.2[c]	1.6	12.8[c]	

[a]Mean of all west coast data presented above.
[b]1 SD.
[c]Difference between west and east coast significant at 95% confidence level.

the northeastern Pacific dogfish relative to the Atlantic form on the basis of vertebral numbers is not appropriate.

MUSCLE AND BLOOD ELECTROPHORESIS

To further examine the possibility of subspecific distinction between dogfish from east and west coasts of North America, muscle myogens and blood hemoglobins were electrophoretically analyzed. Fish of different sizes and both sexes from the same area yielded similar results. Close similarity of muscle myogen patterns from east and west coasts (Fig. 4) indicate that on a

TABLE 3. Vertebral numbers of *S. acanthias* stocks around North and South America showing calculated degree of differentiation between adjacent stocks.[a]

Stocks	No. sampled	Total vertebral no. Mean	1 SD	CD[b]	Overlap (%)
East coast of North America	20	112.5	2.70		
				1.27	21
S South America	5	105.8	2.59		
				1.05	29
West coast of North America	47	100.3	2.67		

[a]Combined data of this study, Springer and Garrick (1964), and Templeman (1944).

[b]CD (coefficient of difference) = mean 1 − mean 2 : SD 1 + SD 2 where mean 1 is the largest (Mayr 1969). Conventional level of subspecific differentiation is 1.28 or greater (20% overlap or less of stock characteristic).

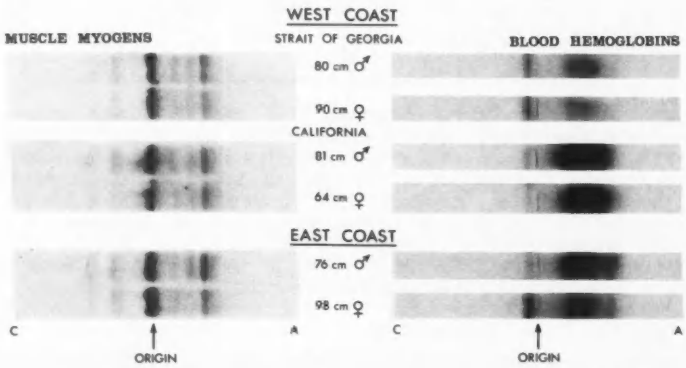

FIG. 4. Comparison of electropherograms of muscle myogens and blood hemoglobins for *S. acanthias* from the east and west coasts of North America. Solutions were introduced at the origins. C, cathode; A, anode.

geological time scale these stocks have only recently become separated, or that some genetic interchange still occurs between them. However, a comparison of blood hemoglobins, which may be more readily adaptable than muscle myogens (Tsuyuki et al. 1965), indicates a difference between the dogfish stocks from the Strait of Georgia and the east coast of North America, with the pattern of the California animals somewhat intermediate. These differences are not attributable to variations between fetal and adult hemoglobins (Manwell 1963), as the dogfish we used were generally of the same size. A gradual change in blood hemoglobins from the northeastern to the southeastern Pacific to the north Atlantic is thus indicated, but the continuity of this change removes any support for subspecific designation of regional stocks. Considering the distribution of *S. acanthias* (Fig. 3) and the movements of tagged animals between stocks, dogfish from any of these areas are likely to be similar.

PELVIC–DORSAL FIN POSITION

Additional evidence against subspecific distinction of dogfish stocks is obtained from the P-D2:D1-P ratio, which, in our data, has a significant ($P < 0.05$) negative regression on length (Fig. 5). Thus, P-D2:D1-P ratio data collected from all areas fall within the 95% confidence limits of the Strait of Georgia data. Though the P-D2:D1-P ratio has contributed to the clarification of the subspecific question for the northeastern Pacific stock of *S. acanthias*, it has also been the source of some confusion in the literature when applied to the separation of species within *Squalus*.

Recent authors (Bigelow and Schroeder 1957; Garrick 1960) have classified all forms of *Squalus*

TABLE 4. Comparison of total body length with the position of the pelvic fins relative to the dorsals (P-D2:D1-P ratio) for the group divisions within the genus *Squalus*.

Group, source, sex	No. sampled	Data range: Body length (*cm*)	Data range: P-D2:D1-P ratio (%)
S. acanthias			
This study — males	80	25.3–97.8	92.1–54.8
— females	102	24.3–122.5	78.7–45.6
Bigelow and Schroeder (1957)	—	—	≥100
Garrick (1960)[a]	8	23–99	293–80
S. blainvillii[b]			
Bigelow and Schroeder (1957)	—	—	<100
Garrick (1960)[a]	6	21–98	327–152
S. megalops-cubensis			
Lindberg and Legeza (1956)[c]	—	—	126
Bigelow and Schroeder (1957)	—	—	>100

[a]Data derived from fig. 2, p. 523.
[b]*S. blainvillii* (Garrick 1960) = *fernandinus* (Bigelow and Schroeder 1957).
[c]Their *S. brevirostris* = *S. megalops* (Garrick 1960); only mean value given.

under one of three major species groups as follows: 1) *S. acanthias*, 2) *S. blainvillii* (*fernandinus*), and 3) *S. megalops-cubensis*. The northeastern Pacific dogfish is placed in the first group based on shape of pectoral fins, position of first dorsal fin relative to pectorals, appearance of external nares, color pattern, and the position of the pelvic fins relative to the dorsals (P-D2:D1-P ratio). Our Strait of Georgia data for this latter characteristic (Fig. 5) indicate that the pelvic fins are closer to the second dorsal than the first, are relatively closer in larger individuals, and are approximately 8% closer for females than males. Similar data from other northeastern Pacific dogfish stocks fall within the 95% confidence limits of our data, as do those from the east coast of North America. However, Bigelow and Schroeder (1957) and Garrick (1960) reported that the pelvic fins were closer to the first dorsal in *S. acanthias* (Table 4). For the *S. blainvillii* group these two authors differ by noting the pelvic position as on opposite sides of the midpoint between the dorsals. In the *S. megalops-cubensis* group Bigelow and Schroeder (1957) and Lindberg and Legeza (1956) noted that the pelvics were closer to the first dorsal than the second. Garrick (1960) confirmed this observation by reporting no difference in pelvic fin position between this group and the *S. blainvillii* group in which the pelvics were also closer to the first dorsal. Our data for this ratio (Fig. 5) suggest that the differences reported by these workers may have resulted from the effects of length and sex. Although the species groups may be separable in other ways, apparently the

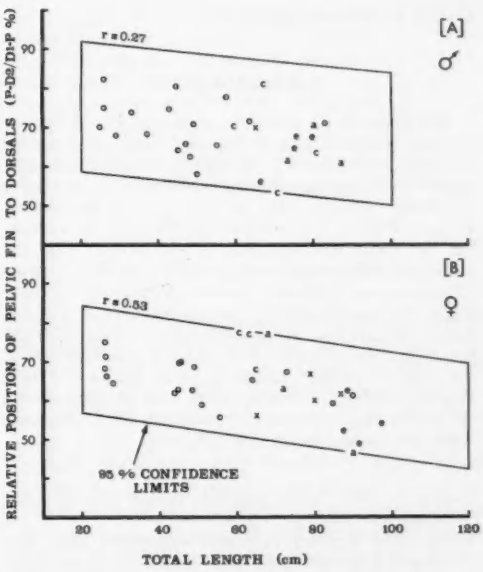

FIG. 5. Relationship of relative position of pelvic fins to dorsal fins and total body length for *S. acanthias*; A) males and B) females. Enclosed areas represent the 95% confidence limits around the Strait of Georgia data (not plotted) for the length ranges sampled. Regressions for ratio on length are R(%) = 77.4–0.102 L (centimeters) for males and R(%) = 73.3–0.145 L (centimeters) for females. Data from Lindberg and Legeza (1956) for the short fin (○) and the long fin (×) forms are superimposed, as are those of this study for the east coast of Canada (e), Alaska (a), and California (c).

P-D2:D1-P ratio substantially overlaps among groups and is therefore of little use in distinguishing species, although its value might be enhanced if supplemented with data on length and sex.

In summary, the value of the morphometric ratios, F:H and P-D2:D1-P, used by other authors to distinguish between subspecies and species groups, respectively, is open to doubt. However, dogfish migration and muscle myogen patterns indicate that the northeastern Pacific Ocean spiny dogfish is one of several stocks comprising the cosmopolitan species, *S. acanthias*. Though the North American east and west coast stocks of dogfish show differences in vertebral numbers and blood hemoglobin patterns, conventional analyses fail to justify subspecific status as a result of overlapping characteristics between these groups and a South American stock which has intermediate characteristics. Thus, the present undivided taxonomic status of *S. acanthias* (Linnaeus) indicated by the American Fisheries Society (Bailey et al. 1970) for the northeastern Pacific dogfish is supported.

Acknowledgments

We thank K. S. Ketchen of the Pacific Biological Station, Nanaimo, B.C., who made data and facilities available to us, and S. J. Westrheim for use of personnel and equipment, and assistance in obtaining specimens. Thanks also go to R. M. F. S. Sadleir, F. J. F. Fisher, N. J. Wilimovsky, and C. C. Lindsey for reviewing the manuscript. Assistance with the electrophoretic work was provided by H. Tsuyuki (Fisheries and Marine Service, Vancouver Laboratory). We also thank T. Jow (California), J. Edgington (Alaska), and E. J. Sandeman (Newfoundland) for collection of specimens, and the management of the former dogfish processing plant, Seafresh Pacific Products Ltd., for allowing us to take samples during 1973–74. This study was supported by a National Research Council grant to G. H. G.

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Early Stages of Some Copepods (Crustacea) Parasitic on Marine Fishes of British Columbia

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KABATA, Z. 1976. Early stages of some copepods (Crustacea) parasitic on marine fishes of British Columbia. J. Fish. Res. Board Can. 33: 2507–2525.

Detailed descriptions and illustrations are presented of the nauplii (the only, or the first nauplius stage) of *Bomolochus cuneatus*, *Holobomolochus spinulus*, *Chondracanthus gracilis*, *Ergasilus turgidus*, *Eudactylina similis*, *Pseudocharopinus dentatus*, and *Haemobaphes diceraus*, and the copepodid stages of *H. diceraus*, *P. dentatus*, and *Nectobrachia indivisa*.

The naupliar morphology of *Ergasilus* is similar to that of free-living Cyclopidae but differs in significant details from that of supposedly related *Bomolochus*. The nauplii of poecilostome and siphonostome copepods are similar. The morphology of the free-living larval stages might offer valuable clues to intrafamilial relationships of Lernaeopodidae. Differences were observed between copepodids of two species of *Haemobaphes*.

KABATA, Z. 1976. Early stages of some copepods (Crustacea) parasitic on marine fishes of British Columbia. J. Fish. Res. Board Can. 33: 2507–2525.

L'auteur décrit et figure en détails les stades nauplius (le seul ou le premier stade nauplius) de *Bomolochus cuneatus*, *Holobomolochus spinulus*, *Chondracanthus gracilis*, *Ergasilus turgidus*, *Eudactylina similis*, *Pseudocharopinus dentatus* et *Haemobaphes diceraus*, et les stades copépodites d'*H. diceraus*, *P. dentatus* et *Nectobrachia indivisa*.

La morphologie du nauplius d'*Ergasilus* est semblable à celle des Cyclopidae pélagiques, mais diffère dans d'importants détails de celle de *Bomolochus*, espèce qu'on suppose apparentée. Les copépodes peocilistomes et siphonostomes ont des nauplii semblables. La morphologie des stades larvaires pélagiques peut nous éclairer sur les relations intrafamiliales des Lernaeopodidae. Nous avons observé des différences entre les stades copépodites de deux espèces d'*Haemobaphes*.

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THE life cycles of parasitic copepods include one or several free-swimming stages which serve for dispersal of the species. These free-swimming stages search out new host individuals and enable the parasite to survive and complete its life cycle. With the progress of adaptation to parasitism, the free-swimming period in the life of parasitic copepods tends to become shorter and less complicated. Consisting of several stages, separated by molts, in more primitive copepods, it is reduced to a single stage in those that can be considered more advanced.

For a fish to become infected, it must come into contact with the infective free-swimming stage, which is most commonly, though not universally, a copepodid. Some knowledge of the life stages, therefore, is beneficial to those concerned with the health of fish. This is especially true in the field of mariculture. As the number of marine fish farms increases, the problems caused by parasites in the operation and efficiency of production begin to be more clearly defined. It is now known that some parasitic copepods can become serious pests of cultured fish. This has been amply demonstrated recently in salmoniculture off the coast of Norway (e.g. Johannessen 1974). It is, therefore, increasingly important that more attention be paid to the dispersal stages of these parasites, since it is they that should be prevented from finding and establishing themselves on the cultured fish. However, our knowledge of the larval stages of marine parasitic copepods is still scanty. They are not at present readily recognizable to the fish culturist, or often even to workers more closely acquainted with parasitic crustaceans.

With this in mind, some work was conducted at the Pacific Biological Station, Nanaimo, B.C., to develop methods of culturing parasitic copepods under laboratory conditions. The work was intended to be the first step in providing experi-

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mental stocks of parasites to be used in the investigation of preventive measures. As a spin-off of this activity, some knowledge of the early larval stages of marine copepods has accumulated over the last 4 yr. The descriptions of these stages given below partially fill the gap in our knowledge and, hopefully, will enable mariculturists to recognize at least some of the potential enemies of the fish in their care. Although not all the species described are harmful to cultured fish, all are of scientific interest, since none of them has been previously described in sufficient detail.

Materials and Methods

The methods by which the larvae were obtained have been described earlier by Kabata and Cousens (1973). They are simpler than is generally imagined, at any rate as far as hatching of the eggs is concerned; it is much more difficult to rear the copepods past the first molt. For some species it has proved, so far, to be impossible.

In some instances, plumules or serrations of setae comprising armature of appendages were omitted from drawings for the sake of clarity. The details of armature are, however, clear from the text.

This paper describes the following copepod stages:

Nauplius	Copepodid
Bomolochus cuneatus Fraser, 1920	*Haemobaphes diceraus* Wilson, 1917
Holobomolochus spinulus (Cressey, 1969)	*Pseudocharopinus dentatus* (Wilson, 1912)
Chondracanthus gracilis Fraser, 1920	*Nectobrachia indivisa* Fraser, 1920
Ergasilus turgidus Fraser, 1920	
Eudactylina similis T. Scott, 1902	
Pseudocharopinus dentatus (Wilson, 1912)	
Haemobaphes diceraus Wilson, 1917	

Nauplii

1. *Ergasilus turgidus* Fraser, 1920

Body oval (Fig. 1), with slightly narrower posterior end carrying balancers less than 20 μ long. Length of 10 specimens 120–140 (mean 124) μ.

First antenna (Fig. 2) indistinctly bipartite, with geniculate flexion near base. Anterior margin with long unarmed seta near border of two parts; posterior margin with minute prickle on distal half. Apical armature of 2 long setae, longer pinnate, ¾ length of antenna, shorter less than half length of latter, with delicate serrations (omitted in figure); 2 minute prickles in anterior corner of apex.

Second antenna (Fig. 3) biramous, with indistinct border between sympod and rami. Basal part of sympod marked off from remainder by constriction and armed on medial margin with comparatively large, strong, slightly unciform and tapering spine, projecting mediad and meeting that of opposite appendage near midventral line. Endopod unsegmented, short, slightly pedunculate, armed with 3 setae: longest about 4 times length of ramus, with row of short spinules on one margin (not shown in figure); slightly shorter second seta unarmed; third seta very short, spiniform. Exopod five-segmented: basal segment constituting about half length of ramus, with long, apparently semipinnate seta in distomedial corner; second segment short, bearing in distomedial corner long seta with finely serrated margins; segments 3 and 4 similar, progressively diminishing in size; segment 5 very small, with 2 apical setae: longer with both margins serrated, shorter unarmed.

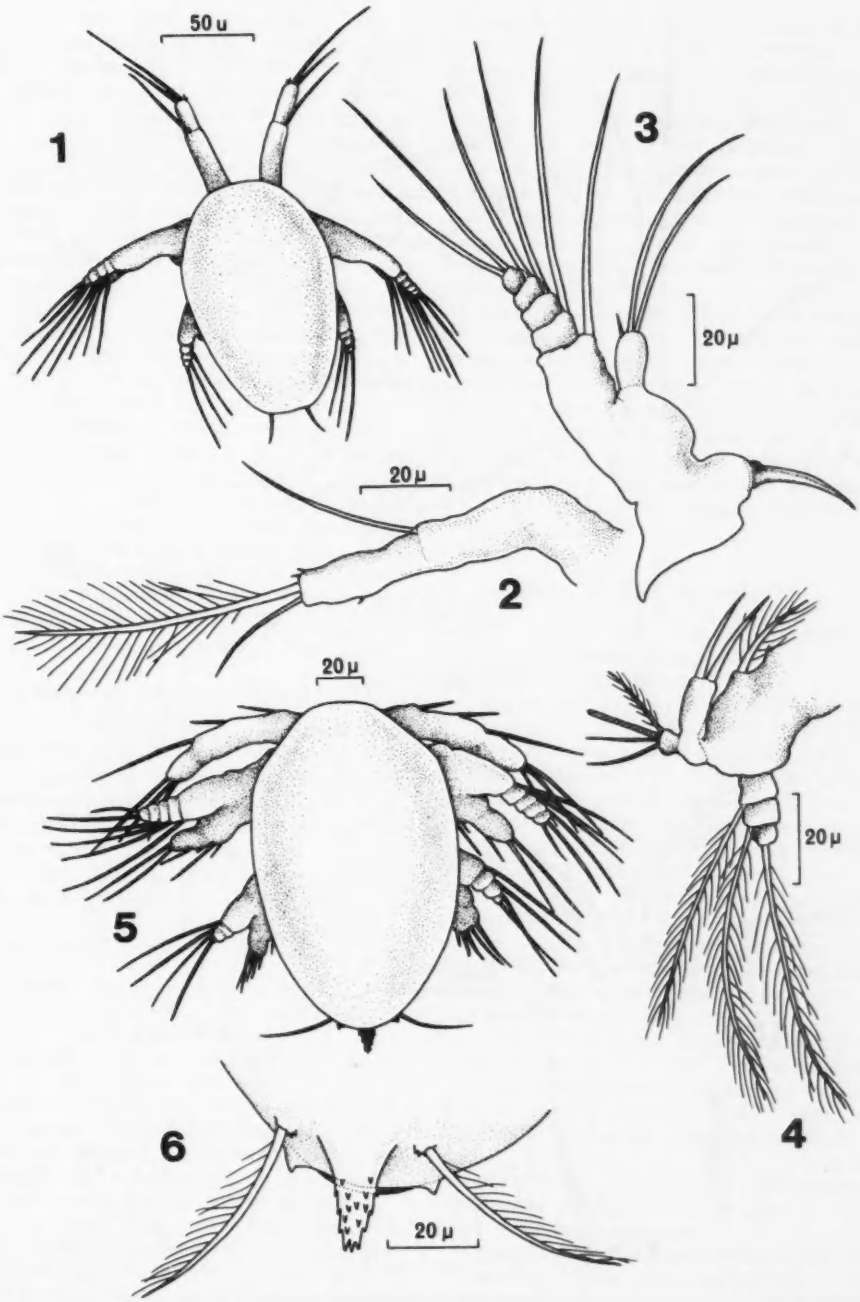
Mandible (Fig. 4) short, squat, biramous, with indistinct borders between sympod and rami. Sympod with 1 short pinnate seta pointing anteriorly on medial margin. Endopod short, indistinctly two-segmented, basal segment with cylindrical masticatory process pointing anteriorly and armed with 2 strong, unarmed, spiniform setae; distal segment short, small, with 4 apical structures: medialmost pinnate seta, next to slender, blunt-tipped structure (aesthete?) and 2 unarmed, slender setae, all 4 of similar length. Exopod three-segmented, segments short, decreasing in size distally, each with long pinnate seta.

2. *Bomolochus cuneatus* Fraser, 1920

Body oval, with narrower posterior end (Fig. 5). Length of 10 specimens 120–160 (mean 146) μ. Balancers semipinnate, about 50 μ long, arising from small swellings with some serrations near bases (Fig. 6). Short posterior median process, slightly tapering and covered with sharp denticles; on both sides and slightly dorsal to process single subtriangular outgrowths.

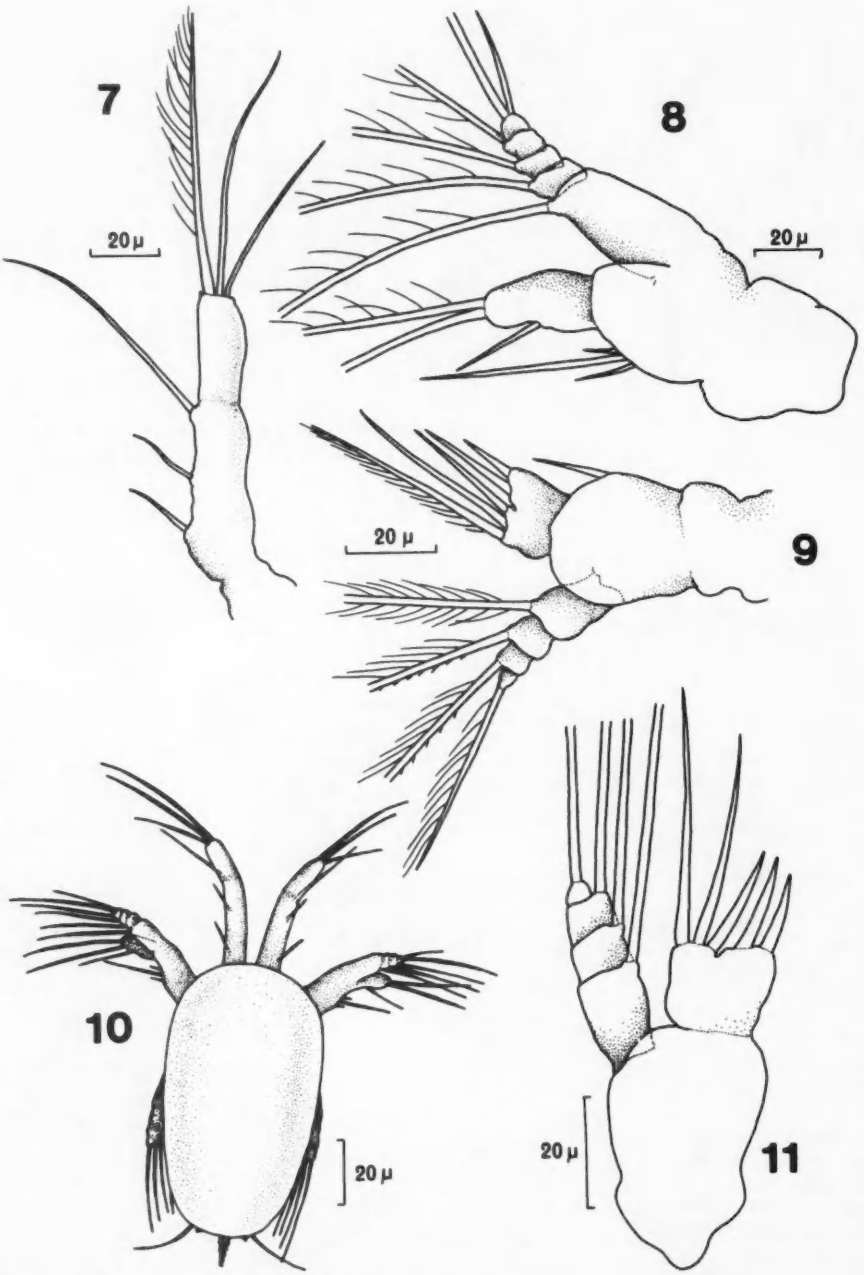
First antenna (Fig. 7) indistinctly bipartite, with geniculate flexion near base. Anterior margin of basal part with 3 unarmed setae, first 2 of about equal length, third more than twice as long; 3 long setae in apical armature: one semipinnate, other 2 somewhat shorter and unarmed; minute prickle in anterior corner of apex (in some specimens 2 such prickles).

Second antenna (Fig. 8) biramous, with borders between sympod and rami obsolete. Indistinct constriction at about half length of sympod. Endopod indistinctly two-segmented; basal segment with 3 unarmed setae, central long one



FIGURES 1–6. *Ergasilus turgidus* AND *Bomolochus cuneatus*.

FIG. 1. *E. turgidus*, nauplius, dorsal; FIG. 2. First antenna, ventral; FIG. 3. Second antenna, ventral; FIG. 4. Mandible, ventral; FIG. 5. *B. cuneatus*, nauplius, dorsal; FIG. 6. Nauplius, posterior process, ventral.



FIGURES 7–11. *Bomolochus cuneatus* AND *Holobomolochus spinulus.*

FIG. 7. *B. cuneatus*, nauplius, first antenna, ventral; FIG. 8. Second antenna, ventral; FIG. 9. Mandible, ventral; FIG. 10. *H. spinulus*, nauplius, dorsal; FIG. 11. Mandible, ventral.

flanked by 2 short ones; distal segment with 1 unarmed seta on medial margin; 2 setae in apical armature, 1 unarmed (perhaps with a few barely visible serrations), other semipinnate, possibly with 1 or 2 denticles at base. Exopod five-segmented, basal segment constituting more than half length of ramus, with semipinnate seta in distomedial corner; segments 2–4 gradually decreasing in size, each with long semipinnate seta; fifth segment very small, with 2 apical setae: one short, tapering and unarmed, other long, possibly with faint serrations on one or both margins.

Mandible (Fig. 9) biramous, with somewhat clavate, indistinctly two-segmented sympod; segment 2 larger than first, with short, sharp, unarmed seta on medial margin. Endopod one-segmented, with slightly bilobed tip; medial lobe with 2 short, unarmed, spiniform setae, lateral lobe with 3 setae increasing in length from medial to lateral side; lateral seta semipinnate, 2 others unarmed. Exopod four-segmented, basal segment constituting about half ramus length, with long pinnate seta in distomedial corner; segments 2 and 3 short, each with long seta in distomedial corner, setae with pinnae along one margin and serrations along other; segment 4 very small, tipped with long, semipinnate seta.

3. *Holobomolochus spinulus* (CRESSEY, 1969)

Body oval, with only slightly narrower posterior end (Fig. 10). Posterior process like that of preceding species, but more slender. Length of 10 specimens 140–160 (mean 145) μ.

Appendages as in *Bomolochus cuneatus*, but no seta on medial margin of sympod. Armature of mandibular endopod (Fig. 11) more robust than that of *B. cuneatus*.

4. *Chondracanthus gracilis* FRASER, 1920

Body almost regularly oval (Fig. 12), with short balancers about 20 μ long. Length of 10 specimens 213–225 (mean 221) μ.

First antenna (Fig. 13) indistinctly bipartite. Anterior margin of basal part with 2 short and 1 long setae, all with both margins denticulated. Apical armature consisting of 3 setae: anterior corner of apex carrying 1 long seta with denticulated margins and 1 very short, unarmed; short, denticulated seta in posterior corner of apex.

Second antenna (Fig. 14) biramous, with squat, apparently unsegmented sympod. Endopod also unsegmented, shorter than exopod, with 2 long apical setae: medial serrated on both margins, lateral with serrations on one margin and pinnae on other (armature not shown in figure). Exopod four- or five-segmented; basal segment constituting more than half total length of ramus, with long pinnate seta in distomedial corner; segments 2 and 3 short, with similar setae; segment 4 indistinctly subdivided into two halves, basal part with short, slender pinnate seta, distal with long seta serrated on both margins and with spiniform outgrowth in lateral corner.

Mandible (Fig. 15) biramous, with endopod shorter than exopod, not clearly delimited from sympod. Latter somewhat pedunculate, apparently unsegmented. Endopod indistinctly two-segmented, basal segment shorter than distal, unarmed; distal segment with rounded apex bearing 2 long setae, medial one serrated on both margins, lateral one half pinnate, serrated along one margin; short, spiniform outgrowth in medial corner. Exopod four-segmented; basal segment more than half length of ramus, with long, pinnate seta in distomedial corner; segments 2 and 3 small, each with long semipinnate seta serrated along one margin; short, rounded segment 4 with similar seta on apex.

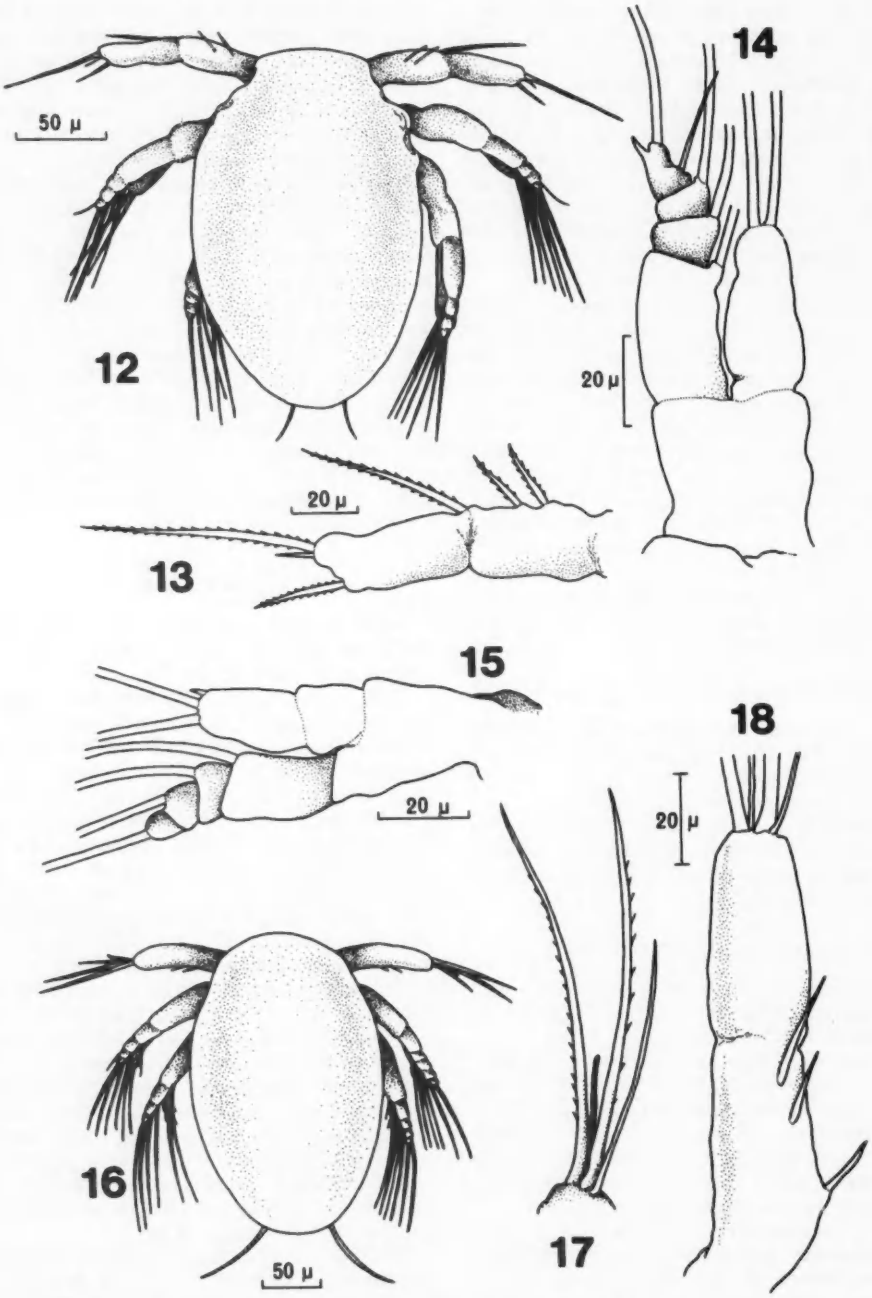
5. *Eudactylina similis* T. SCOTT, 1902

Body roughly oval (Fig. 16), length of 10 specimens 220–260 (mean 246) μ. Balancers comparatively long, about 70 μ.

First antenna (Fig. 18) indistinctly bipartite; proximal part with 3 rather short, unarmed setae on anterior margin; distal part with 4 structures in apical armature (Fig. 17): 2 long setae serrated along one margin, short unarmed seta and even shorter, slender and blunt seta (sensory?).

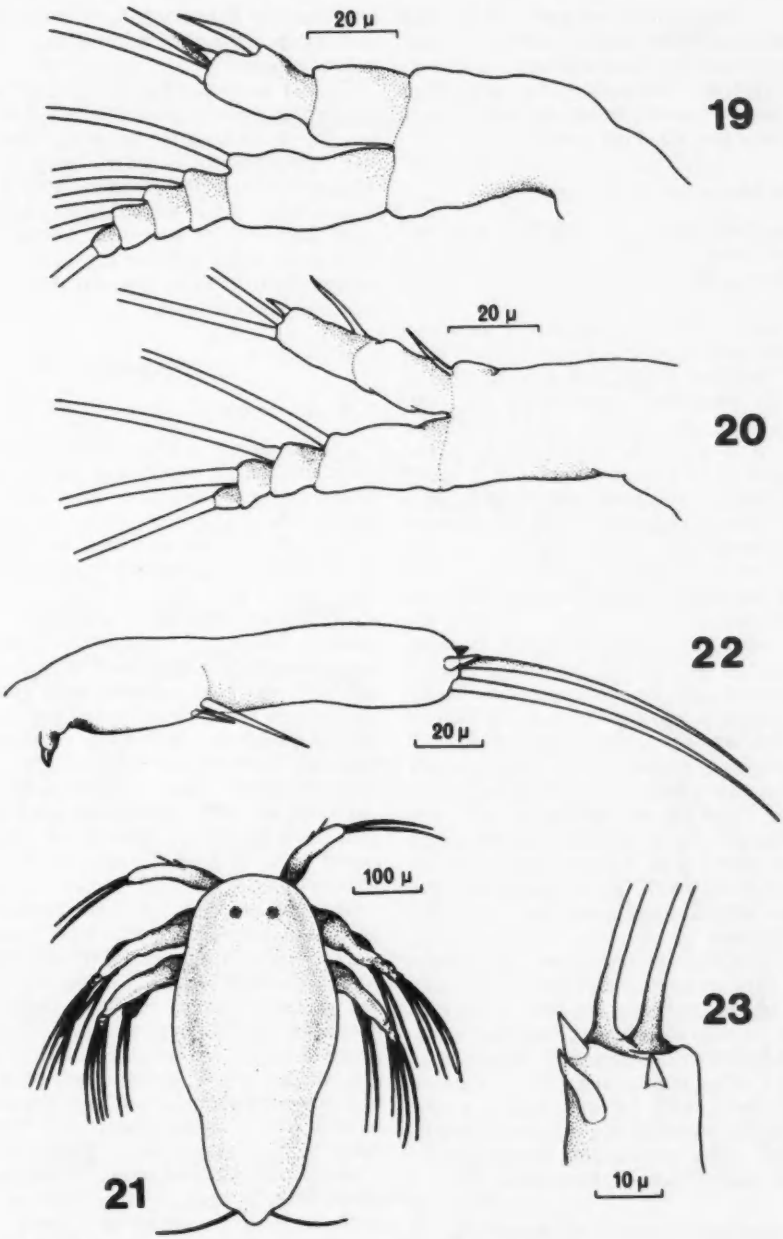
Second antenna (Fig. 19) biramous, with rami indistinctly divided from sympod; latter with slight geniculate flexion near base, somewhat pedunculate. Endopod indistinctly two-segmented, segments about equally long; basal segment unarmed; terminal with strong spiniform seta on medial margin; apical armature consisting of 2 long setae with one margin serrated and the other provided with pinnules; short dentiform process at base of medial of 2 setae. Exopod longer than endopod, five-segmented, basal segment more than half length of ramus, with 1 long seta in distomedial corner; segments 2–4 small, decreasing in size, all with single long seta in distomedial corner; segment 5 very small, subconical, with similar seta on apex; all setae semipinnate, serrated along one margin.

Mandible (Fig. 20): Sympod about half length of appendage, with short, unarmed seta at base of endopod. Rami indistinctly divided from sympod. Endopod indistinctly two-segmented, basal segment unarmed, terminal with 1 short, unarmed seta near base; apical armature con-



FIGURES 12–18. *Chondracanthus gracilis* AND *Eudactylina similis.*

FIG. 12. *Ch. gracilis*, nauplius, dorsal; FIG. 13. First antenna, ventral; FIG. 14. Second antenna, ventral; FIG. 15. Mandible, ventral; FIG. 16. *E. similis*, nauplius, dorsal; FIG. 17. Apical armature of first antenna, ventral; Fig. 18. First antenna, ventral.



FIGURES 19–23. *Eudactylina similis* AND *Haemobaphes diceraus.*

FIG. 19. *E. similis*, nauplius, second antenna, ventral; FIG. 20. Mandible, ventral; FIG. 21. *H. diceraus*, nauplius, dorsal; FIG. 22. First antenna, ventral; FIG. 23. First antenna, apex, dorsal.

sisting of 1 short, spiniform seta and 2 long semipinnate ones, with serrations along one margin. Exopod longer than endopod, four-segmented, segments diminishing in size from proximal to distal, each bearing long, semipinnate seta with serrations along one margin.

6. *Haemobaphes diceraus* WILSON, 1917

Body pyriform (Fig. 21), with narrower posterior end. Length of 10 specimens 368–394 (mean 382) μ. Balancers relatively long, about 100 μ.

First antenna (Fig. 22) indistinctly bipartite; at base short subcylindrical process tipped with claw-like denticle, ventral margin with 2 unequally long setae, both semipinnate and with serrations along one margin (not shown in figure); 2 setae in apical armature, long and armed like those on proximal part; also 3 dentiform outgrowths in subapical position (Fig. 23).

Second antenna (Fig. 24) biramous, borders between sympod and rami indistinct or not observable. Sympod robust, unsegmented, and unarmed. Endopod indistinctly two-segmented (in some specimens no intersegmental division observable); basal part longer, unarmed; terminal with 1 unarmed seta on medial margin and 2 long semipinnate setae on apex, both with minute serrations along one margin. Exopod indistinctly three- or four-segmented, basal segment about ⅔ of total length, cylindrical, with 1 semipinnate seta in distomedial corner; segment 2 short, about equally long and wide, with similar seta in same position; segments 3 and 4 not distinctly separated from each other, both with similar setae; all setae semipinnate, with serrations along one margin and inflated base fitting into spoon-like cavity of segment.

Mandible (Fig. 25) biramous, rami not clearly delineated from sympod; latter more than half length of appendage, more or less cylindrical; slender seta at base of endopod. Endopod indistinctly two-segmented, segments of about equal length, basal segment unarmed; distal segment with slender seta twice its own length arising near base; apical armature of 2 long semipinnate setae serrated along one margin; dentiform outgrowth near base of lateral apical seta.

7. *Pseudocharopinus dentatus* (WILSON, 1912)

Body subspherical (Fig. 26), with inflated ventral surface. Balancers absent. Length of 10 specimens 300–360 (mean 340) μ.

First antenna (Fig. 27) unsegmented, subcylindrical, with loose cuticular sheath irregularly wrinkled; 3 long apical setae, 1 slender and much shorter than other 2, all unarmed; 2 small and sharp denticular outgrowths, 1 apical, the other subapical.

Second antenna (Fig. 28) biramous, with no observable intersegmental borders. Loose cuticular sheath irregularly wrinkled, differing from one specimen to another. Sympod unarmed. Endopod shorter than exopod, with 2 long, unarmed apical setae. Exopod with 5 similar setae.

Mandible (Fig. 29) short, uniramous, with geniculate flexure at about half length, apparently unsegmented, in loose cuticular sheath. Two long unarmed setae at apex.

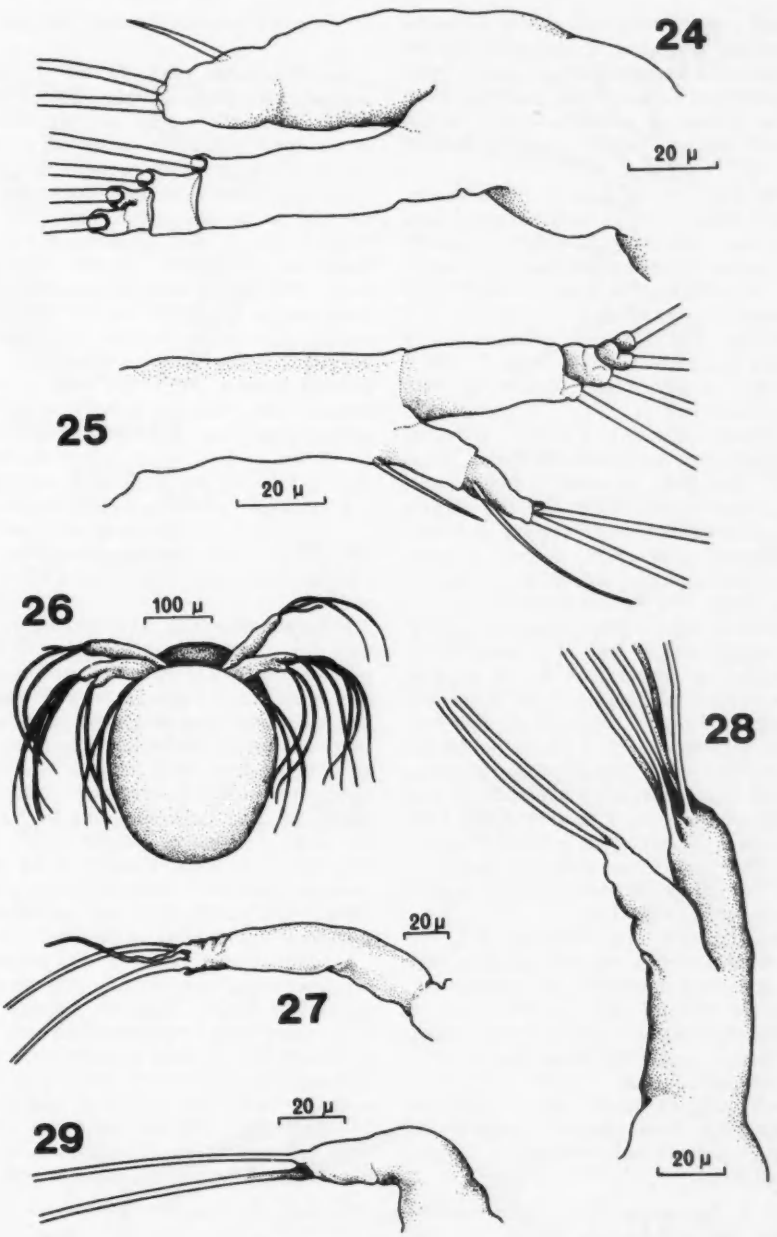
Copepodids

1. *Haemobaphes diceraus* WILSON, 1917

Cephalothorax (Fig. 30) fusiform, with rounded anterior margin and slightly converging lateral margins extended into short posterolateral lobes; 1 sensory setule on both lateral margins, pair of similar setules on dorsal surface in posterolateral corners. Posterior part of body consisting of 4 divisions. Second leg-bearing segment broader than long, about half width of posterior margin of cephalothorax, with convex lateral margins. Third leg-bearing segment similar but narrower than second, with rudiments of third legs in form of spiniform setae. Fourth leg-bearing segment indistinctly delimited from genitoabdomen, devoid of leg rudiments. Genitoabdomen larger than preceding segment, subquadrangular, with slightly convex lateral margins, posterior margin bisected by anal slit and armed with uropods. Length of 10 specimens 465–560 (mean 515) μ.

First antenna (Fig. 32) with obscure segmentation and geniculate flexion near base; anterior margin with 3 long, slender, unarmed setae. Apical armature (Fig. 31) consisting of anterior and posterior groups of setae; anterior group dominated by slightly subapical, long, blunt-tipped aesthete; in apical position 1 very long seta divided into 2 almost down to base, 1 of branches with sharp, other with blunt tip; close to that seta 3 other structures, 1 slender and fairly long, 1 robust, short, sharp-pointed, and 1 slender, blunt, and short; 3 long setae on dorsal side of apex, 1 very short at base of aesthete. Posterior group of 4 setae, all more slender than those of anterior group: 3 long (1 divided to base) and 1 very short. All setae unarmed.

Second antenna (Fig. 33) subchelate, robust, with body indistinctly divided into 2 by constriction. Basal part longer than terminal, with vestige of exopod protruding from margin, irregularly



FIGURES 24–29. *Haemobaphes diceraus* AND *Pseudocharopinus dentatus.*

FIG. 24. *H. diceraus,* nauplius, second antenna, ventral; FIG. 25. Mandible, ventral; FIG. 26. *P. dentatus,* nauplius dissected from egg, ventral; FIG. 27. First antenna, ventral; FIG. 28. Second antenna, ventral; FIG. 29. Mandible, ventral.

wrinkled and covered with soft cuticle. Terminal part presumably consisting of endopod, bearing subchela and with extended distal corner; inner corner of extension hollowed out, unarmed. Long slender seta at base of subchela. Latter robust, tapering, with narrow flanges on either side of its hooked tip.

Mandible (Fig. 34) of 2 parts: basal shorter and broader than terminal, subcylindrical, unarmed; terminal flat distally, with rounded tip and 7 teeth in dentiferous margin; all teeth about same size and shape. (In Fig. 34 distal part slightly damaged by handling.)

First maxilla (Fig. 35) with endopod longer than exopod, subconical, distally with 2 slender unarmed setae; exopod shorter, similar but with only 1 apical seta.

Second maxilla (Fig. 36) of 2 parts, articulating with each other by elbow-like joint. Basal part robust, apparently unarmed. Terminal part of similar length, more slender, apically slightly expanded, unarmed, with rudimentary claw not clearly delimited; claw short, slightly curving, with rows of setules on each side of distal half.

First leg (Fig. 37) biramous, with two-segmented sympod. Basal segment unarmed, distal with long, slender seta at base of exopod. Endopod one-segmented, longer than broad, expanding distally, with 6 pinnate setae on distal and medial margins. Exopod longer than endopod, much broader distally, with 1 spine on lateral margin; 3 pinnate setae and 3 other structures (Fig. 38) on distal margin (1 semipinnate seta serrated along one margin, 1 short seta with both margins serrated, and 1 very short spiniform seta, unarmed). First pair of legs linked by a complicated system of interpodal bars, interlocking with those of second pair (Fig. 41).

Second leg similar to first. Endopod (Fig. 39) identical with that of first leg; exopod (Fig. 40) with 3 pinnate setae distally, 1 semipinnate serrated along one margin, and 1 short with both margins serrated. (Another spiniform seta usually present on lateral margin not shown in Fig. 40.)

Uropod (Fig. 42) with 2 pairs of pinnate setae, 1 pair in each distal corner (pinnules omitted). Between them 1 short unarmed seta and 1 short process of unknown nature, apparently soft and blunt.

2. *Pseudocharopinus dentatus* (WILSON, 1912)

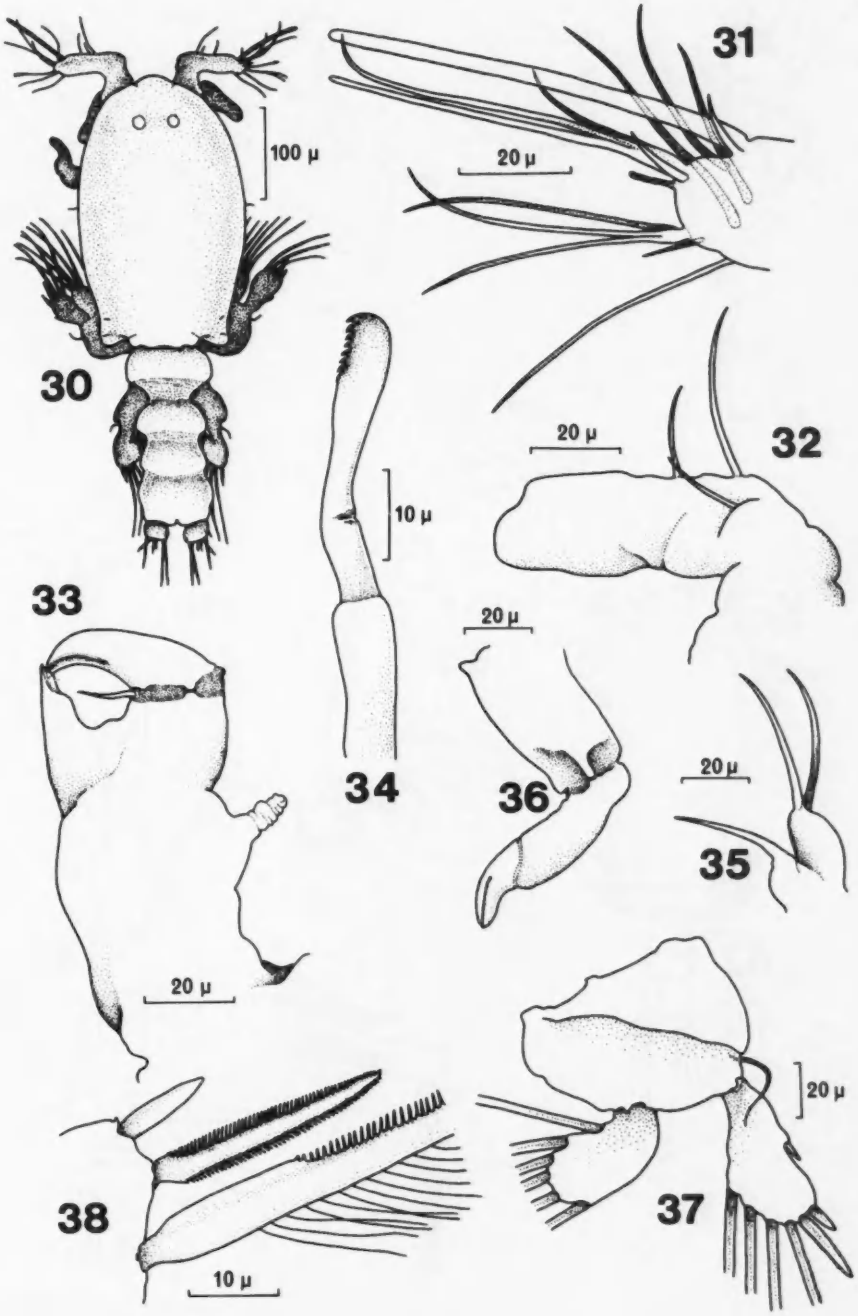
Cephalothorax (Fig. 43, 44) oval in dorsal outline, with posterior and anterior ends somewhat truncated; uneven and shallow crescentic groove near midlength on dorsal surface, marking obsolete boundary between maxilliped- and first leg-bearing segments. Lateral margins just anterior to dorsal groove with pair of minute setules. Dorsal part of posterior margin with flange-like projection. Second leg-bearing segment with lateral margins converging and posterior margin regularly concave from dorsal side; softer part below tergum subcylindrical and bearing 2 minute setules (Fig. 56). Third leg-bearing segment (Fig. 56) with posterior part broader than anterior; pair of setules on dorsal surface; third legs rudimentary, papilliform, bearing 2 setae each. Last free thoracic segment slightly broader than long, with divergent lateral, and straight anterior and posterior margins. Genitoabdomen subquadrate, with posterior margin split by anal slit; minute setules on dorsal surface. Length of 10 specimens 620–660 (mean 640) μ.

First antenna (Fig. 45) obscurely segmented, with two or three constrictions, differing from specimen to specimen, with geniculate flexion near base; anterior margin with 3 naked setae, 2 long ones near base and third short, pointed, at about midlength. Subapical group consisting of very long aesthete, with setule at base and 1 long, sturdy seta. Apical armature consisting of 2 groups of setae: anterior group of 3 short, slender setae, 1 somewhat longer, and 1 long seta, near center of apex, close to wide, robust one (another aesthete?); posterior group of 4 slender setae, 1 split nearly to its base; additional 2 subapical and shorter setae on posterior margin.

Second antenna (Fig. 46, 47) biramous, with indistinctly two-segmented, sturdy sympod; basal segment of sympod unarmed, terminal with strip of denticles across ventral surface and extending to lateral side. Exopod one-segmented, bulbous, with slightly pedunculate base; tip with 3 long, unarmed setae and patch of minute prickles. Endopod (Fig. 48) two-segmented; basal segment with row of blunt, digitiform spines (usually about 10); terminal segment with powerful

FIGURES 30–38. *Haemobaphes diceraus.*

FIG. 30. Copepodid, dorsal; FIG. 31. Apex of first antenna, dorsal; FIG. 32. First antenna, dorsal; FIG. 33. Second antenna, medial; FIG. 34. Mandible, lateral; FIG. 35. First maxilla, lateral; FIG. 36. Second maxilla, lateral; FIG. 37. First leg, ventral; FIG. 38. First leg, distolateral corner of exopod.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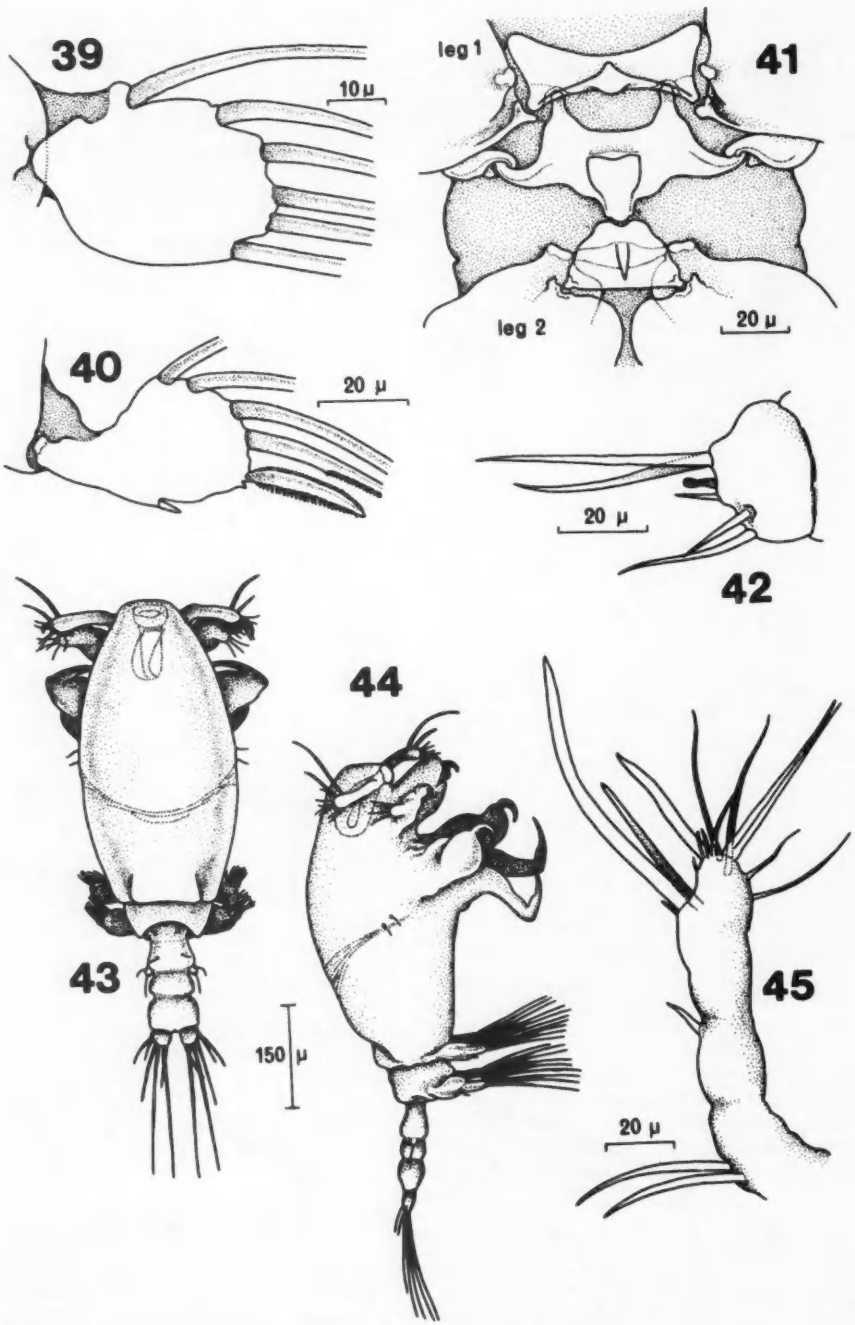
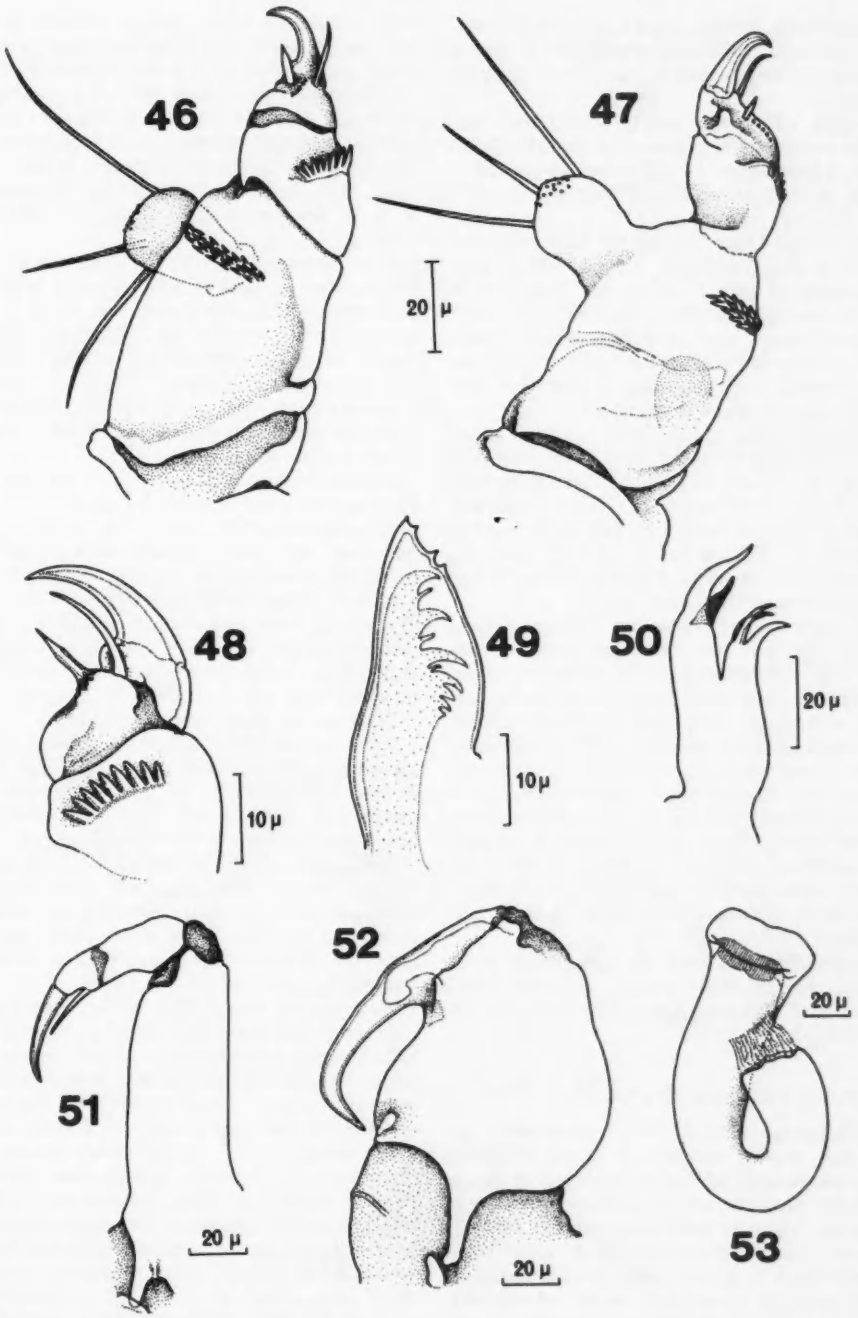


FIGURES 39–45. *Haemobaphes diceraus* AND *Pseudocharopinus dentatus.*

FIG. 39. *H. diceraus*, second leg, endopod, ventral; FIG. 40. Second leg, exopod, ventral; FIG. 41. Interpodal bars, ventral; FIG. 42. Uropod, dorsal; FIG. 43. *P. dentatus*, copepodid, dorsal; FIG. 44. Same, lateral; FIG. 45. First antenna, dorsal.



FIGURES 46–53. *Pseudocharopinus dentatus.*

FIG. 46. Second antenna, ventral; FIG. 47. Same, lateral; FIG. 48. Second antenna, endopod, medial; FIG. 49. Mandible, lateral; FIG. 50. First maxilla, medial; FIG. 51. Maxilliped, medial; FIG. 52. Second maxilla, medial; FIG. 53. Frontal filament, ventral.

prehensile hook, slender seta on one side of hook, shorter, stronger, spiniform seta on other; row of very small serrations medial and ventral to spiniform seta.

Mandible (Fig. 49) short, squat, with few irregular serrations in region of future dentiform margin. (Appendage of following stage visible through cuticle; its dental formula P1, S1, P1, S1, P1, S1, B3.)

First maxilla (Fig. 50) clearly biramous, exopod shorter than endopod, tipped with 3 processes; endopod with 2 similar but more robust processes. Second maxilla (Fig. 52) subchelate; body short, squat, and powerful, unarmed; thin cuticle on base permitting flexibility of articulation; subchela long, unciform, not divided into shaft and claw, apparently unarmed.

Maxilliped (Fig. 51) slender, longer than second maxilla, subchelate, with body unarmed. Subchela with shaft indistinctly divided into 2: longer basal part unarmed, shorter terminal carrying a barb on inner margin; claw slender, long, barb more than half length of claw; no other armature observed. Frontal filament (Fig. 53) short, thick, with one flexure.

Two pairs of swimming legs similar. Second leg (Fig. 54) with two-segmented sympod, connected with opposite leg by complicated system of interpodal bars; basal segment unarmed, segment 2 with slender seta next to base of exopod. Latter short, distally broader, with 1 spiniform seta on lateral margin; fairly short, unarmed, spiniform seta in distolateral corner, medial to it one half pinnate seta and 3 long pinnate ones. Endopod shorter than exopod, with 6 pinnate setae (pinnules omitted). Exopod of first leg (Fig. 55) with additional spiniform seta in distolateral corner. Endopod of first leg with 7 pinnate setae.

Uropod (Fig. 56) with 2 large pinnate setae on distal margin, short pinnate seta on dorsal surface above 1 of large setae; 3 shorter setae on lateral margin.

3. *Nectobrachia indivisa* FRASER, 1920

Cephalothorax (Fig. 57, 58) with rounded anterior and slightly converging lateral margins; slight indentations of lateral margins at about midlength; posterior end of dorsal surface protruding in ridge-like eminence. Frontal filament (Fig. 64) short and straight, with small basal plug and much larger terminal plug. Second leg-bearing segment about half width of cephalothorax, short, with concave margin of tergum; lateral margins converging. Third leg-bearing segment with convex lateral margins, less than half width of preceding segment, about equally long and broad, with 2 minute setules on dorsal surface (Fig. 69). Third leg rudimentary, papilliform, surmounted by 2 setae. Next segment subquadrangular, about same size as preceding one, unarmed; genitoabdomen quadrangular, equal in size to preceding segment, with 2 minute setules on dorsal surface near posterior margin (Fig. 69). Total length of copepodid, according to S. N. Wilkes (unpublished data), 580–660 (mean 630) μ.

First antenna (Fig. 59) indistinctly segmented; anterior margin with 2 long unarmed setae near base, one similar but shorter seta distal to them and very long aesthete on distal half, equalling length of entire appendage; slender, unarmed seta near base of aesthete; posterior margin with 1 slender seta near apex; 5 long, slender, unarmed setae in apical armature, 2 of them split nearly to their bases.

Second antenna (Fig. 60) biramous, with sympod obscurely segmented, unarmed. Exopod one-segmented, digitiform, much shorter than endopod, with 3 long, slender setae on apex and patch of fine denticles among bases of setae. Endopod long, two-segmented, slender, and cylindrical; basal segment ⅔ length of ramus, unarmed; distal (Fig. 61) apparently capable of articulation with basal segment, short, with powerful hook and 2 slender setae on apex.

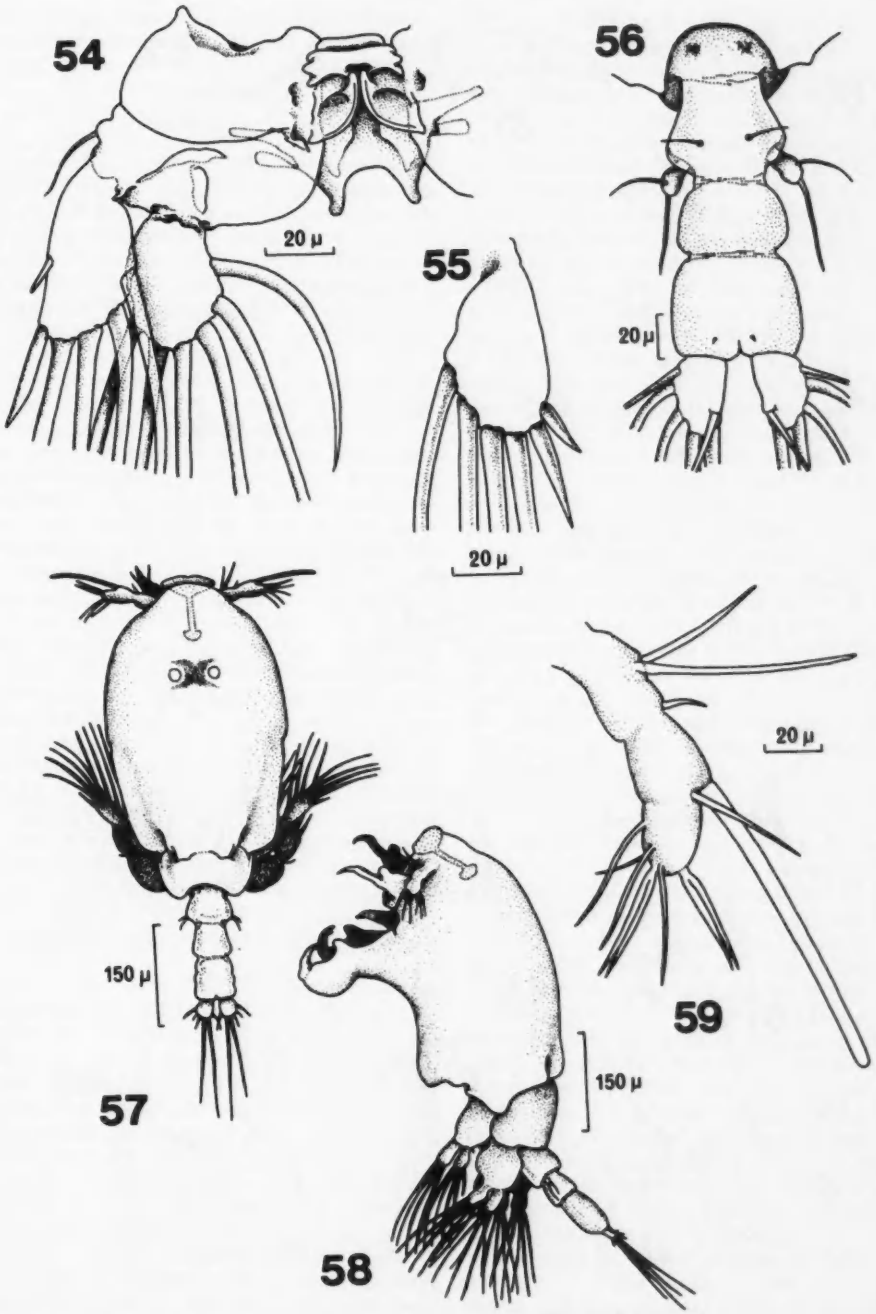
Structure of mandible not determined.

First maxilla (Fig. 62) short, conical, with 2 tapering apical processes of about equal length. Second maxilla (Fig. 63) short, unsegmented, distally attenuated, with blunt tip; vesicle-like outgrowth (possibly artifact) on distal half.

Maxilliped (Fig. 65) subchelate. Body robust, medial margin with shelf-like expansion near base, margins of shelf denticulated. Subchela cylindrical, slightly bent, with short unciform claw and slender barb shorter than claw. No other armature observed.

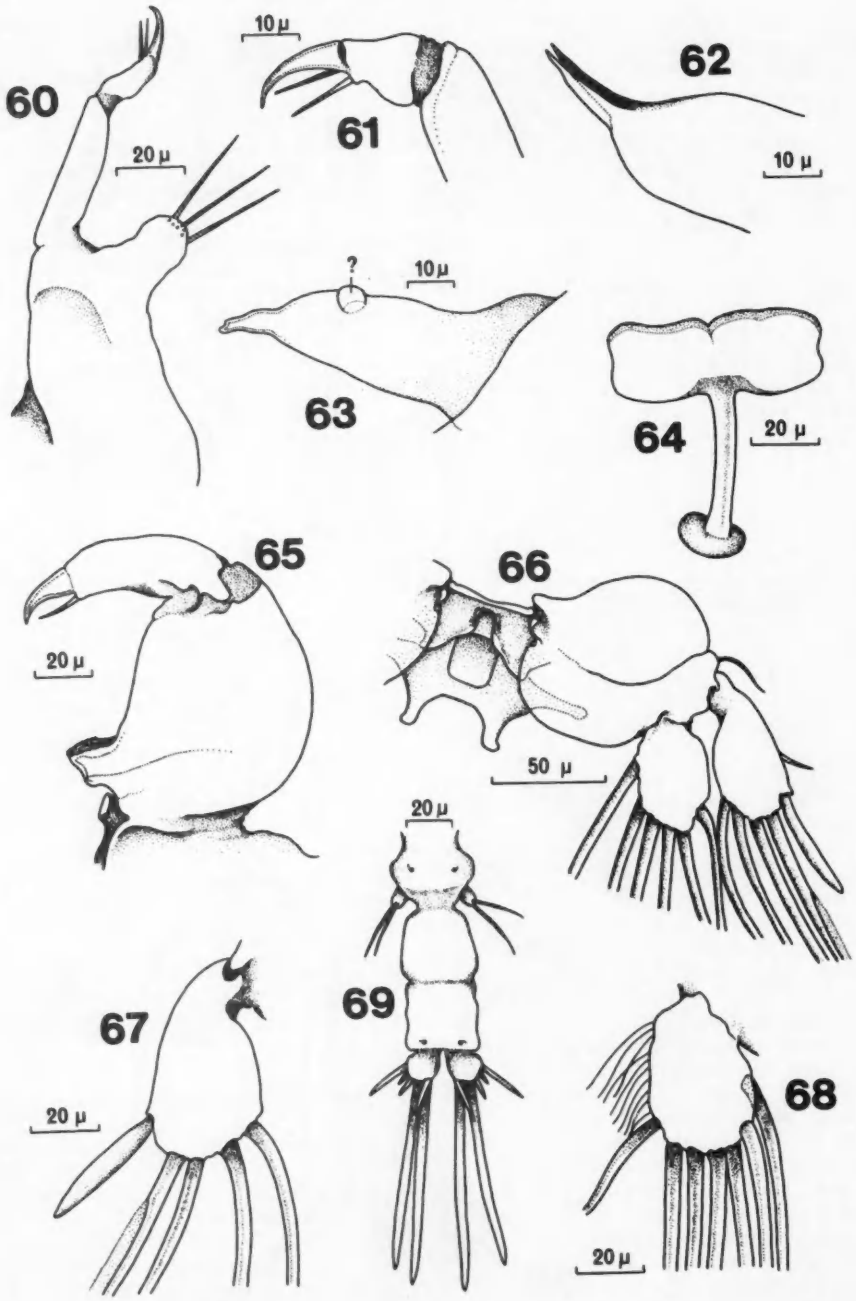
Two pairs of legs similar. Second leg (Fig. 66) connected with opposite appendage by interpodal bar. Sympod two-segmented; basal segment unarmed, second with slender seta lateral to base of exopod. Exopod with narrow base, expanding distally; slender, short seta on lateral margin; distal margin with 1 medium-long, blunt-tipped, unarmed seta, 1 long, semipinnate seta with strip of membrane along one margin, 3 pinnate setae. Endopod shorter, more stocky than exopod, with fringe of setules on lateral margin (omitted in figure), with 6 pinnate setae on distal and medial margins. First leg similar, but exopod (Fig. 67) without slender setae on lateral margin and endopod (Fig. 68) with 7 pinnate setae.

Uropod (Fig. 69) with 6 structures; distal



FIGURES 54–59. *Pseudocharopinus dentatus* AND *Nectobrachia indivisa*.

FIG. 54. *P. dentatus*, second leg, dorsal; FIG. 55. First leg, exopod, dorsal; FIG. 56. Posterior part of body, dorsal; FIG. 57. *N. indivisa*, copepodid, dorsal; FIG. 58. Same, lateral; FIG. 59. First antenna, ventral.



FIGURES 60–69. *Nectobrachia indivisa.*

FIG. 60. Second antenna, lateral; FIG. 61. Second antenna, tip of endopod, lateral; FIG. 62. First maxilla, ventral; FIG. 63. Second maxilla, lateral; FIG. 64. Frontal filament, ventral; FIG. 65. Maxilliped, medial; FIG. 66. Second leg, dorsal; FIG. 67. First leg, exopod, ventral; FIG. 68. First leg, endopod, ventral; FIG. 69. Posterior part of body, dorsal.

margin with 2 long, robust, semipinnate setae; 3 short setae on lateral margin, and 1 similar seta on dorsal surface above medial pinnate seta.

Discussion

Bomolochus cuneatus and *Holobomolochus spinulus* (Fig. 5, 10) belong to Bomolochidae, a family with completely unknown ontogeny, but quite probably their life cycle contains more than one nauplius stage. The newly hatched first nauplii described here both carry peculiar posterior processes (Fig. 6, 10) which probably can be used as distinguishing features of bomolochid nauplii in general.

The nauplius of *Ergasilus turgidus* (Fig. 1) is also the first instar. All its significant features resemble those of other *Ergasilus* nauplii of that stage. Ergasilid nauplii have two morphological characteristics which distinguish them from the corresponding stages of other parasitic copepods: their second antenna carries a prominent spine on the medial side of the base (Fig. 3), and the short, squat mandible has its gnathobase armed with 2 spiniform setae projecting mediad from the basal segment of its endopod (Fig. 4). A similar mandible is present in the nauplius of *Thersitina* (Pagenstecher, 1861). It is, therefore, quite possible that this type of mandible is common to all Ergasilidae.

Ergasilidae appear to have much in common with the free-living Cyclopidae with regard to their naupliar morphology (Gurney 1933), but are quite different in this respect from the bomolochids. Ergasilidae and Bomolochidae are believed to be closely related; they were treated in the past as subfamilies of one family. In the light of differences between their nauplii, it seems that their relationship with each other should be reexamined.

Prior to this work, only two chondracanthid nauplii were known. Claus (1858) described the nauplius of *Chondracanthus lophii* and Heegaard (1947) of *Acanthochondria cornuta*. The work of the latter author suggests, without definitely proving, that the life cycle of Chondracanthidae contains only one nauplius stage. In any event, the nauplius of *C. gracilis* (Fig. 12) described in this paper is the first stage after hatching. It resembles in most characteristics the two previously known species.

All the nauplii mentioned above belong to poecilostome copepods. The remaining three nauplii described in this paper are the early stages of siphonostome copepods. The nauplius of *Eudactylina similis* (Fig. 16) is the second one known for this genus. The first was described by Wilson (1922) for *E. nigra*. Wilson's description was, however, rather brief and provided no information on the structure of the appendages. I was unsuccessful in proceeding by culture beyond the first nauplius stage. This was regrettable because Eudactylinidae are among the most primitive siphonostome parasites and a knowledge of their life cycle, and, in particular, of the morphology of the copepodid stage, might prove to be of considerable interest from the point of view of the phylogeny of parasitic copepods in general.

The early stages of *Haemobaphes diceraus* (Fig. 21) resemble those of *H. cyclopterina*, as described by Heegaard (1947). The characteristic feature of the first stage nauplius is a previously unknown claw-like spine arising from a papilliform outgrowth at the base of the first antenna (Fig. 22). I know of no other nauplius with a similar claw on the first antenna.

What is currently known about the early stages of Lernaeopodidae presents a rather confusing picture. The tendency towards reduction of the preparasitic phase of development is generally recognized. It is reflected in the poor development of the nauplius, which is always devoid of balancers, and often of the mandible. In some lernaeopodids this stage is passed through within the egg, the parasite hatching as a copepodid, ready to become attached to the host. However, this tendency is apparently far from prevailing, judging from Table 1 which summarizes the literature data on this topic.

The first seven species shown in Table 1 belong to the freshwater branch of Lernaeopodidae and are related to one another (Kabata and Cousens 1972). One of them appears to have a free-swimming nauplius. Nordmann's (1832) record of that nauplius in *Achtheres percarum* is, however, highly suspect; his statement that *Tracheliastes polycolpus* also has a free-swimming nauplius was later proved erroneous by Vejdovsky (1877). Wilson (1911) found that in *A. ambloplitis* the nauplius remained in the egg. It can be expected that other species of *Achtheres* have much the same development. (It is noteworthy that Wilson misunderstood Nordmann as saying that *A. percarum* did not have a free-swimming nauplius.) There is no disagreement on the fact that the freshwater lernaeopodids do not possess a naupliar mandible.

Two species in Table 1 belong to the *Charopinus*-branch of Lernaeopodidae, a rather primitive branch of the family, parasitic primarily on skates and rays (Kabata and Cousens 1972). I dissected the nauplius of *Pseudocharopinus dentatus* from the egg. (The species hatches as the copepodid stage.) The only other reported

TABLE 1. Naupliar characters of some Lernaeopodidae species.

Species	Nauplius free	Nauplius in egg	Mandible	Balancers	Reference
Salmincola edwardsii		×	—	—	Dedie (1940)
S. californiensis		×	?	?	Kabata and Cousens (1973)
S. salmoneus		×	?	?	Friend (1941)
Achtheres percarum	×		—	—	Nordmann (1832)
A. ambloplitis		×	—	—	Wilson (1911)
Basanistes huchonis		×	?	?	Kollar (1835): *fide* Gurney (1947)
Tracheliastes polycolpus		×	—	—	Vejdovsky (1877)
Lernaepoda galei	×		+	—	Gurney (1947)
Charopinus dalmanni	?	?	+	—	Turner and Wilson (1862)
Pseudocharopinus dentatus		×	+	—	present paper
Clavella adunca	×		—	—	Shotter (1971)
Brachiella impudica		×	?	?	Gurney (1947)
Nectobrachia indivisa	×		+	—	S. N. Wilkes (unpublished data)

nauplius of this branch was that of *Charopinus dalmanni*, described by Turner and Wilson (1862) who stated: "In some of those ova the larva could be studied at the stage immediately preceding the rupture of the ovum; in other cases the free larvae were obtained." Gurney (1947) considered it evidence that at least some of the eggs hatch at the nauplius stage. The text, however, is ambiguous and I believe that these authors "obtained" their nauplius by dissection, as I did. As in the freshwater branch of the family, it is difficult to believe that two closely related species can show such great differences in their ontogeny. In both instances the naupliі had a rudimentary and poorly developed, but unmistakably present, mandible.

The *Lernaeopoda*-branch of the family is represented in Table 1 by only one species, *Lernaeopoda galei*, which possesses, according to Gurney (1947), a free-swimming nauplius and mandible. The aberrant *Nectobrachia indivisa*, probably related to the *Clavella*-branch of the family, resembles *Lernaeopoda* on both counts, but *Clavella adunca*, although hatching at the nauplius stage, has no mandible. Next to nothing is known about the *Brachiella*-branch of the family. Gurney's (1947) suggestion that one of the species of this group (*B. impudica*) has no free nauplius has not been followed by additional information.

Heegaard (1947) used the naupliar mandible as one of the main features distinguishing between his Fistulata and Pectinata, taxa corresponding roughly to the poecilostome and siphonostome copepods, respectively. According to him the naupliі of the former have mandibles with two-segmented endopods, whereas the corresponding ramus in the mandible of the latter consists of three segments. This study failed to corroborate Heegaard's findings. The mandibles of the poecilostomes *Ergasilus turgidus* (Fig. 4), *Bomolochus cuneatus* (Fig. 9) and *Chondracanthus gracilis* (Fig. 15) indeed had two-segmented endopods. The segmentation, however, was not always clear, the ramus sometimes appearing as completely unsegmented. The same was true of the two naupliar mandibles of the siphonostomes, *Eudactylina similis* (Fig. 20) and *Haemobaphes diceraus* (Fig. 25). The segmentation was often difficult to detect, and, where detectable suggested that the endopod consists of not more than two segments.

The examination of the copepodid stage larvae also led to several interesting observations. One of them concerns differences between the copepodids of two species of *Haemobaphes*, *H. diceraus*, studied in this paper, and *H. cyclopterina* as described by Heegaard (1947). The second antenna of *H. diceraus* has reached the level of development comparable to that of the adult appendage, from which it differs only in the presence of a vestigial exopod (Fig. 33). In contrast, the second antenna of the copepodid of *H. cyclopterina* appears much less advanced, particularly in the structure of its subchela. The second difference is in the structure of the mandible. Heegaard's fig. 86 shows the mandible of *H. cyclopterina* as consisting of a bulky sympod, surmounted by a short, three-segmented exopod and a long, slender endopod modified into the mandibular blade. The mandible of *H. diceraus*, however (Fig. 34), is an almost perfect replica of the adult appendage. Several other apparent differences between the two species (e.g. armature of swimming legs and uropods) might be attributable to the differences in the methods of observation and illustrating conventions.

The other two copepodids described here

(*Pseudocharopinus dentatus* and *Nectobrachia indivisa*) belong to the family Lernaeopodidae. The former is the first to be described for the *Charopinus*-branch of the family. One of its interesting features is the first maxilla (Fig. 50) which clearly shows the biramous nature of this appendage.

The aberrant condition of *N. indivisa* is manifest at this stage in some of its appendages. The second antenna (Fig. 60) is distinguished by the unusually long and slender endopod, apparently with a joint-like articulation between the penultimate and distal segments (compare with the more usual copepodid second antenna of *P. dentatus* in Fig. 47). I was unable to study in detail the mandible of *N. indivisa*, but Wilkes (unpublished thesis) reported that it is much reduced at this stage. Both pairs of maxillae are also reduced. The first maxilla (Fig. 62) is unique among lernaeopodid copepodids described so far. The second maxilla (Fig. 63) is even more unusual. In other known copepodids of this family it is either subchelate (see Fig. 52), or ends in a broad, denticulated, pad-like plate, as in the *Clavella*-branch (Shotter 1971). In *N. indivisa* it appears to taper to a blunt point and is quite unarmed.

Comparisons of these two copepodids with published data on others belonging to Lernaeopodidae have shown that several types can be recognized by the morphology of their appendages. The copepodid of the *Charopinus*-branch has a prominent aesthete in the apical armature of its first antenna (Fig. 45). The known copepodids of the freshwater branch, *Salmincola* and *Achtheres* (cf. Kabata and Cousens [1973] and Wilson [1911], respectively) have no such structure. The copepodid of *Clavella*, a representative of yet another branch of the family, lacks an aesthete but that of *Nectobrachia*, seemingly a relative of that branch, has a very prominent one (Fig. 59).

Although no definite conclusions can yet be made on the basis of copepodid morphology as to the intrafamilial relationships of Lernaeopodidae, the differences discussed above suggest that their morphology might be a useful indicator of these relationships.

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Natural Water and Chemical Budgets for a Small Precambrian Lake Basin in Central Canada

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Results of a 4-yr study of the hydrology of the Rawson Lake watershed, as well as the chemistry of precipitation, streamflow, and the lake are presented. Inputs of water and most chemicals varied by as much as 2 times from one year to the next, illustrating that several years' data are necessary to determine accurately average nutrient inputs and losses from an ecosystem. Precipitation appeared to be almost the sole source of P and N to lake and terrestrial ecosystems, although N_2 fixation cannot be dismissed in the latter case. Significant proportions of Ca, Mg, Na, K, Cl, and SO_4 were supplied directly from precipitation. The lake also received substantial quantities of these elements as well as silicon, from weathering of terrestrial geological materials. Although far from any major industrial sources of SO_2, the pH of precipitation averaged <5 for the years studied. Both terrestrial and lake systems retained a high proportion of entering P and N, and smaller proportions of other nutrients. Interpretation of relative retentions of nutrients revealed that the terrestrial ecosystem has well-balanced P and N supplies, while the lake was P limited. Rates of loss of chemicals from the terrestrial watershed of Rawson Lake are comparable to other sites in the Precambrian Shield, but lower than values from other geological settings.

SCHINDLER, D. W., R. W. NEWBURY, K. G. BEATY, AND P. CAMPBELL. 1976. Natural water and chemical budgets for a small Precambrian lake basin in central Canada. J. Fish. Res. Board Can. 33: 2526–2543.

Le présent article traite des résultats d'une étude de 4 a. sur l'hydrologie du bassin hydrographique du lac Rawson, de même que sur la chimie des eaux de précipitation, d'écoulement et du lac lui-même. D'une année à l'autre, les apports en eau et en la majorité des produits chimiques ont varié du simple au double, démontrant ainsi la nécessité de recueillir des données durant plusieurs années afin de déterminer avec précision les moyennes du bilan des éléments nutritifs d'un écosystème. Le phosphore et l'azote des écosystèmes terrestre et lacustre ont semblé provenir presque exclusivement des précipitations (bien qu'il ne faille pas négliger le phénomène de fixation de l'azote). Des quantités appréciables de Ca, Mg, Na, K, Cl et SO_4 ont aussi été apportées directement par les précipitations. Le lac a aussi reçu un apport important de ces éléments, de même que de silicium provenant de l'altération superficielle de matériaux terrestres par les agents atmosphériques. Malgré l'éloignement des sources industrielles de SO_2, le pH des précipitations a été, en moyenne, inférieur à 5. Les systèmes terrestre et lacustre ont accumulé une grosse fraction de l'apport en phosphore et en azote et des quantités moins élevées des autres éléments nutritifs. L'interprétation des retentions relatives des éléments nutritifs a indiqué un bon rapport P/N dans l'écosystème terrestre tandis que dans le lac, le phosphore était un facteur limitant.

Les taux de déperdition en éléments chimiques dans les sols du bassin hydrographique du lac Rawson se comparent à ceux d'autres régions du bouclier précambrien, mais sont inférieurs à ceux d'autres types de terrains.

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"It is self-evident that the nature of the drainage area must in a large measure determine the kinds and amounts of primary nutritive material in a lake. The composition, age and weathering of the rock, the soil and vegetation cover, the extent of the drainage area and the amount of run-off are all important considerations." D. S. Rawson, 1939.

PROCESSES that affect the rates of geochemical weathering and nutrient cycling are of fundamental interest to ecologists, limnologists, and managers of terrestrial and aquatic ecosystems, since the supplies of vital elements to biotic communities determine their productivity and degree of eutrophication.

These processes and rates for any watershed are ultimately related to the hydrological regime, as well as to relief, geology, climate, and terrestrial flora. Their gross features may be examined by measuring flow rates and chemical concentrations in various components of the hydrological system.

The purpose of this paper is to present data on amounts of major ions and nutrients entering a small natural watershed in the Canadian Precambrian Shield over a period of 4 yr, and to describe how these amounts are modified by chemical weathering, hydraulic transport, biological uptake, and sedimentation as the major ions and nutrients pass through the terrestrial portion of the watershed and then through a small lake. The information has been gathered as part of a larger study of the effects of increased nutrient input on lakes (see Vol. 28, No. 2 and Vol. 30, No. 10 of this journal).

Previous Investigations

Only Schindler and Nighswander (1970), Armstrong and Schindler (1971), Schindler and Fee (1973), Schindler et al. (1973b), and Schindler et al. (1974) have published nutrient input and output from terrestrial drainages and a lake within the same watershed, as well as chemical patterns within the lake. Their calculations are for P, N, and C, only. No such study has previously been carried out for major ions. None of the above studies is for a period of over 1 yr.

Several of the individual components of a watershed budget have previously been studied. Atmospheric sources of ions have been studied by Ahl (1966), Ahlgren (1967), Carroll (1962), Dillon (1974), Gorham (1955, 1958, 1961), Herman and Gorham (1957), Johnson and Owen (1971), Likens (1972), Mackereth (1965), Schindler et al. (1974) and others too numerous to mention here. Armstrong and Schindler (1971) and Barica and Armstrong (1971) give preliminary data for precipitation chemistry in the Experimental Lakes Area (ELA). Schindler and Fee (1974) summarized data for five sites at different latitudes.

Ionic budgets for terrestrial ecosystems underlain by silicate rocks have been studied by Bormann, Likens, and colleagues (Bormann et al. 1968, 1969; Johnson et al. 1968; Likens and Bormann 1972, 1974; Likens et al. 1967, 1970, 1971; Hobbie and Likens 1973), by Bricker et al. (1968), by Fredriksen (1972), Grier and Cole (1972), Cleaves et al. (1970), and Dillon and Kirchner (1975). Brunskill et al. (1971) have given preliminary estimates of weathering rates for major cations in the Rawson Lake basin, based upon very limited hydrological and geochemical data. Of the above authors only Hobbie and Likens (1973), Schindler and Nighswander (1970), and Dillon and Kirchner (1975) have included P, the element of particular interest to limnologists (Vollenweider 1968).

The mechanisms of chemical weathering of silicate minerals have been studied by many investigators including Feth et al. (1964), Garrels and Howard (1957), Garrels and MacKenzie (1967, 1971), Harrie and Adams (1966), Helgeson (1971), Kramer (1966), Stumm and Morgan (1970), and others. The chemistry of groundwater in granitic rocks has been investigated by Garrels (1967) and Garrels and MacKenzie (1967).

Numerous limnologists have studied the distribution of major ions and nutrients in the water column and interstitial waters of lakes in terrain formed primarily of silicate minerals (for example, Einsele 1938; Hutchinson 1957; Mortimer 1941, 1942, 1971). Armstrong and Schindler (1971), Brunskill et al. (1971), Lerman and Brunskill (1971) and Schindler et al. (1971, 1973b) have published similar studies for the Experimental Lakes Area.

Description of the Watershed

The Rawson Lake (L. 239) Watershed is centrally located in the Kenora Experimental Watershed (Fig. 1), in the Environment Canada ELA approximately 60 km southeast of Kenora, Ontario (see fig. 1 in Brunskill and Schindler 1971). The Rawson Lake watershed occupies 396 ha and is underlain by discontinuous Pleistocene deposits over granitic Precambrian bedrock. Pleistocene deposits range from clays and extensive sand deposits in valley bottoms to thin bouldery tills and lag deposits on ridges. Most of the detailed geological and hydrological work in the area has been concentrated in the drainage area tributary to Rawson Lake.

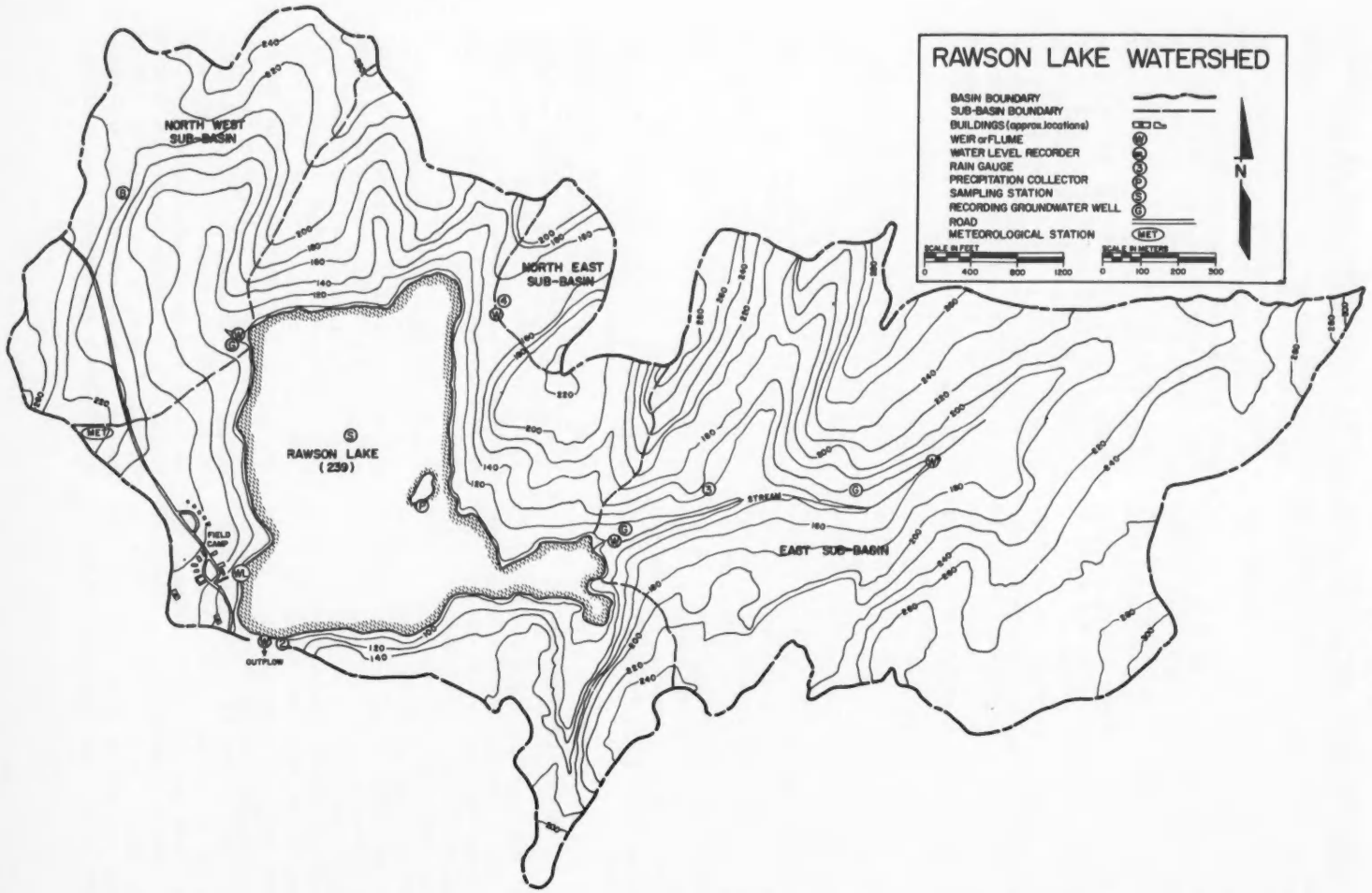

FIG. 1. Topographic map of the Rawson Lake watershed, showing subbasins and locations of hydrological equipment. Contour intervals are in feet.

TABLE 1. Drainage areas for the Rawson Lake watershed, in hectares. Data were obtained planimetrically from Fig. 1.

		% of terrestrial drainage	% of total drainage
NW subbasin	62.83	18	16
E subbasin	170.41	50	43
NE subbasin	9.50	3	2
Undefined drainage	99.35	29	25
Total terrestrial drainage	342.09		86
Lake area	54.28		14
Total drainage	396.37		

Rawson Lake receives runoff from three subbasins which discharge into the lake by way of small streams. These drainage areas are referred to as the northwest (NW), northeast (NE), and east (E) subbasins (Fig. 1, Table 1). The E subbasin, which drains about 50% of the terrestrial portion of the Rawson Lake basin, has a well-defined stream channel up to 1 m deep and 1.5 m wide in the lower part of the subbasin. Discharge from the E subbasin varied from 0 to over 77,000 m^3/wk during 4 yr of study.

The NW subbasin drains about 18% of the terrestrial part of the Rawson Lake basin. A poorly defined stream channel runs from the lake to a trail 30 m west of the shoreline. In the low-lying part of the subbasin above the trail essentially all of the runoff occurs beneath a cover of moss and a surficial organic soil horizon. Discontinuous surface runoff occurs over areas of bedrock outcrop along the steeply sloping segments of the subbasin periphery. Discharge varied from 0 to 35,000 m^3/wk during 4 yr of study.

The NE subbasin occupies about 3% of the terrestrial part of the basin. Water discharges from the subbasin by way of a poorly defined, discontinuous channel that extends across a trail and then disperses into a network of surface rills and subsurface drainage channels within a scattered boulder lag deposit. Discharge from the NE subbasin varied between 0 and 53,000 m^3/wk during three seasons of study. This stream was not monitored in 1970.

The three subbasins described above comprise 71% of the terrestrial part of the Rawson Lake watershed. The remaining 29% of the basin drains directly into Rawson Lake by way of surface runoff across bedrock outcrops near the shore and by way of groundwater seepage through thin deposits of siliceous beach sand, gravel, and boulder lag deposits.

Outflow from the watershed drains through Rawson Lake into Hayes Lake (L. 240) to the south by way of a natural channel 0.5 m deep and 1–2 m wide cut into the sandy spit between the two lakes. Hayes Lake drains across a bedrock outcrop into a stream system that feeds into Dryberry Lake and ultimately into the Lake of the Woods–Winnipeg River system.

The basin is largely forested with 75–100-yr-old jackpine (*Pinus banksiana*) and black spruce (*Picea mariana*) as well as a high percentage of white birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*). Black alder (*Alnus rugosa*) predominates in low-lying areas. Peat and sphagnum mats up to 2 m thick occur in low-lying areas of the NW and NE subbasins.

On July 7, 1973, a violent storm, with winds in excess of 160 km/h, blew down a high percentage of trees in the area. Losses of trees taller than 10 m were up to 30% in the NW and NE subbasins, and over 50% in the E subbasin. On June 26, 1974, the area was burned by a forest fire. This study, therefore, serves as a background for analyzing the effects of these two important natural events (D. Schindler et al. unpublished data). More detailed information about the climate, terrestrial vegetation, and several limnological parameters for the watershed and lake is given in a special issue of this journal, Vol. 28, No. 2, 1971.

GEOLOGY

Bedrock in the Rawson Lake watershed is over 70% grandiorite groundmass. One sample analyzed by Brunskill et al. (1971) had lower Ca, Fe, and Mg, but higher Al and Na than samples from other areas of the Precambrian Shield. Other elements were similar to average Shield values. Bedrock outcrops are numerous on ridges and valley slopes throughout the watershed. Overburden, where it occurs, is usually <1 m deep.

Pleistocene deposits are thicker in low-lying areas, from 2 to 15 m deep. Surface sediments are usually medium to fine silicate sand. Deeper deposits contain some clay fractions, including small quantities of calcite and dolomite. These may be sediments from glacial Lake Agassiz. Due to their high solubility relative to silicate minerals, these calcareous fractions appear to contribute significantly to the chemical composition of groundwater, despite their low abundance in the watershed. The overall groundwater system exhibits properties of a combined silicate–carbonate weathering system. A detailed geological analysis and a description of the reconnaissance technique is provided by Bottomley (1974) and Kennedy (1974).

Limnology

Rawson Lake is a typical dimictic unproductive Precambrian Shield lake. Its area is 54.28 ha (Brunskill and Schindler [1971] give an area of 56.1 ha, but the area 54.28, from more complete survey data, is correct), with a mean depth of 10.5 m and a maximum depth of 30.4 m. The lake is strongly stratified for most of the ice-free season. The hypolimnion remains oxic throughout the stagnation period. Additional information on the lake is given by Brunskill and Schindler (1971) and other papers in 28(2) and 30(10) of this journal.

Meteorology

Climatological data recorded at nearby stations in Kenora and Emo, Ontario, has been summarized by Brunskill and Schindler (1971). The Rawson Lake meteorological station (Fig. 1) was constructed in the ELA in 1969; since its construction, the data collected have been reported in the Meteorological Records.

Materials and Methods

Hydrometric Instrumentation

A hydrometric network was installed in the Rawson Lake watershed in late 1969 and 1970 to monitor precipitation, streamflow, and groundwater. Instrumentation initially included a recording weir on the NW subbasin, a water-level recorder on Rawson Lake, 5 recording and 8 manual precipitation collectors, and a network of 45 nests of piezometers and 20 groundwater wells. In 1971, a Parshall flume for making outflow measurements was installed at the outflow of Rawson Lake and metered daily. During major events, more frequent streamflow measurements at controlled sections were made to obtain detailed hydrographs. Locations of instruments used in this investigation are shown in Fig. 1. Other instrumentation in the Kenora Experimental Watershed was used as well for confirming calculations and assumptions made for the Rawson Lake watershed. More detailed information on the installations and their operation has been reported annually in the *Annual Report* series for the Kenora Watershed (Newbury and Beaty 1969, 1970, 1971, 1972, 1973).

Water Sampling

Streams and groundwater — Weekly samples were collected from the outlets of streams in the NW and E subbasins and at the outlets of Rawson Lake during the open-water seasons of 1970–1973. The NW and E subbasins were also sampled daily during several storm periods in 1971 and 1972. Samples were collected in clean polyethylene bottles and taken to the field laboratory within a few hours. Water temperatures were measured at the time of sampling with a mercury thermometer.

Water samples were collected from piezometers by means of a weighted tube and a manual vacuum pump. Prior to sampling, the water in each of the piezometers was removed so that fresh water from the intake zone would enter the piezometer. This procedure was believed to eliminate the effect of water that might have seeped into the intake zone from overlying strata near the piezometer pipe.

Two to three liters of water were obtained for each sample from most of the piezometers. To obtain the full sample volume it was often necessary to de-water the piezometers more than once. Turbid samples were centrifuged to remove most of the suspended solids before submitting to the analytical laboratory.

Lake — Rawson Lake was sampled every 2nd wk and occasionally more frequently in connection with biological investigations. Samples for chemical analysis were collected from depths of 0, 1, 2, 3, 5, 7, 10, 15, 20, 25, and 30 m at the location shown in Fig. 1 with a plexiglass van Dorn bottle. A temperature profile was taken at the time of sampling with a Whitney thermistor probe.

Atmospheric input — Bulk precipitation for chemical analysis was collected on the island in Rawson Lake during the ice-free season and on the site of the meteorological station during winter. A 0.25-m^2 collector constructed of plexiglass was used in each case. A small net of nylon window screening (mesh = 1.5 mm) over the drain from the collector was used to exclude occasional leaves, twigs, and other large particles. The collector was located approximately 1 m above the ground to eliminate ground contamination. In summer, rain and all dust falling since the previous rainfall were funneled into a 20-liter carboy and analyzed within a few hours after each rainfall, or daily during periods of prolonged precipitation. For winter, a polyethylene bag was affixed to the collector outlet. Each day or after each snowfall, snow caught by the collector was pushed into the bag with a clean plexiglass paddle, sealed, dated, and stored in a deep freezer. Once each month, the snow samples were melted and analyzed.

Analytical Chemistry

Within an hour of collection samples were filtered through Whatman GE/C glass fiber filters and analyzed for molybdate-reactive P, total dissolved P (TDP), $NO_3 + NO_2$-N, NH_3-N, total dissolved N (TDN), SO_4^{2-}, Cl^-, and dissolved organic C (DOC). Reactive silicate, dissolved inorganic carbon (DIC) total Fe, and pH were done on unfiltered samples. Aliquots of sample were preserved with HCl for later determination of the major cations (K^+, Na^+, Ca^{2+}, Mg^{2+}). Filters used for lake, stream, and precipitation samples were analyzed for particulate C, N, and P.

The analytical methods used in the above analyses are described by Armstrong and Schindler (1971), Schindler et al. (1971), and Stainton et al. (1974). Dissolved inorganic C (DIC = dissolved $CO_2 + H_2CO_3 + HCO_3^-$ and CO_3^{2-}) was analyzed by gas chromatography (Stainton 1973). The carbon species, CO_2 gas + H_2CO_3, HCO_3^-, CO_3^{-2}, and the partial

pressure of CO_2 were calculated using the total CO_2, temperature and pH values (Park 1969) and dissociation constants given by Garrels and Christ (1965); H^+ concentrations were measured with a Radiometer pHM4 meter as pH at the time samples were analyzed for total CO_2 (usually within a few hours of sampling). Samples were usually slightly supersaturated with CO_2 so that pH values so obtained are slightly (0.1–0.2 units) lower than at air equilibrium (D. Schindler unpublished data).

Calculation of Water and Chemical Budgets

To determine the chemical budget of Rawson Lake it was necessary to measure the quantities of water in each of the major components of the hydrologic system surrounding the lake shown in Fig. 2. One-week summary intervals for the water budget components were chosen to correspond with the frequency of chemical sampling from streams.

The groundwater inflow and outflow components of the water budget were estimated by D'Arcy's approximation combined with average hydraulic gradient values obtained from the piezometer and well network (Davis and DeWiest 1966). Permeability values were estimated from water-level response tests in the piezometers and the grain-size characteristics of the Pleistocene deposits in the shoreline zones. Bottomley (1974) and Kennedy (1974) give more detailed information.

Chemical data were obtained for precipitation, streamflow from the NW, NE, and E subbasins, the outflow from Rawson Lake, and the water column of Rawson Lake. It was necessary to estimate physical and chemical inputs from areas of undefined drainage by extrapolation from averages for the measured stream subbasins to make an overall estimate for input to the lake. This was accomplished by analyzing the peak hydrographs for each basin for baseflow and interflow or direct runoff components. The residual term in the lake water budget was interpreted as evaporation. This value compared favorably to indirect approximations of evaporation from pan measurements and mass transfer equations with some modification during the breakup and freezeup periods (Newbury and Beaty 1974).

Inflow from the subbasins from January to early April was negligible in all years because streams were frozen. Casual observations of the discharge suggested that the total flow during this period was <1% of the total annual inflow to the lake. It was therefore ignored for these calculations. In a typical year snowmelt begins in early April. By the end of April almost all of the snow has left the terrestrial portion of the watershed by streamflow and overland flow into Rawson Lake. Nonfreezing hydrologic conditions prevail from early May to mid-November. A detailed discussion of the water budget for the basin is given by Newbury and Beaty (1973).

There were short periods during early spring or late fall in all years except 1973 when chemical analysis of the Rawson Lake outflow samples was not done. Average chemical concentrations for the remainder of the year were used to correct outflow data for this omission. Flow during these periods ranged from 19 to 22% of the annual total, based on 1973 results. Because concentration varied little with rate of flow, the error involved in making this extrapolation would not alter our conclusions significantly.

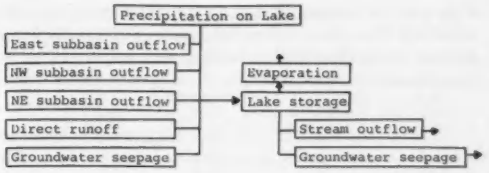

FIG. 2. Major components of the hydrologic system surrounding Rawson Lake.

Results and Discussion

Water Budgets and Turnover Times for Lake 239

Annual precipitation at the main meteorological site ranged from 0.701 to 0.967 m in 1970–1973 (Table 2). The amount falling was similar at all rain gauges, except for occasional localized storms. Precipitation in all 4 yr was higher than averages for Kenora and Emo, the two nearest meteorological stations with long-term data (Brunskill and Schindler 1971, table 2). Total runoff into Rawson Lake in the 4 yr ranged from 0.223 to 0.354 m/yr, higher than given by the Hydrological Atlas of Canada (1969) for the area. Highest flow rates were recorded in the few weeks following spring snowmelt each year, except for 1972, when high flows also followed two rainy periods. There was very little time lag before changes in water input were reflected in water outflow from the lake (Fig. 3). Evapotranspiration ranged from 0.449 to 0.670 m. Lake evaporation was 0.285 to 0.562 m/yr, slightly lower than expected (Bruce and Weisman 1967). As a result, the water renewal times for Rawson Lake are shorter than originally anticipated, ranging from 4.2 to 7.2 yr, instead of the 20 yr predicted from Kenora meteorological data and runoff and evaporation figures from the above references (Brunskill and Schindler 1971).

The E subbasin was the major source of runoff water to the lake, furnishing 44–58% of the total input from terrestrial outflows in the 4 yr of record (Fig. 3 and Table 2). Direct inflows contributed 21–32%, and the NW subbasin 16–23% to the total water budget. In the 3 yr it was studied, the NE subbasin contributed 3–5% to the budget.

Groundwater flow and chemical input via groundwater directly to the lake were found to be negligible in the budgets for the whole lake.

TABLE 2. Parameters in the annual water budget for the Rawson Lake watershed, 1970–73. Average Lake volume corrected from Brunskill and Schindler (1971) is 57.2×10^5 m³. Evaporation in the lake and evapotranspiration plus storage in the terrestrial watershed were calculated by difference.

	1970		1971		1972		1973	
	m³	m	m³	m	m³	m	m³	m
Terrestrial Drainage								
Precipitation	3,308,010	0.967	2,746,983	0.803	2,398,051	0.701	2,541,729	0.743
E Subbasin	496,323	0.291	528,493	0.310	409,892	0.240	461,218	0.271
NW Subbasin	189,490	0.302	274,256	0.436	128,716	0.205	127,877	0.204
NE Subbasin	—	—	37,511	0.395	31,590	0.332	40,212	0.423
Undefined Drainage	330,973	0.333	370,506	0.373	192,130	0.193	171,506	0.173
Total Runoff	1,016,786	0.297	1,210,767	0.354	762,328	0.223	800,813	0.234
Evapotranspiration + Storage	2,291,224	0.670	1,536,216	0.449	1,635,723	0.478	1,740,916	0.509
Rawson Lake								
Precipitation	516,261	0.951	428,672	0.790	347,177	0.689	396,595	0.731
Inflow	1,016,786	1.873	1,210,767	2.231	762,255	1.404	800,813	1.475
Evaporation	262,066	0.483	217,302	0.400	299,958	0.553	152,103	0.280
Outflow	1,210,565	2.230	1,436,889	2.647	797,447	1.469	1,044,417	1.924
Storage	60,416	0.111	−14,752	−0.027	39,027	0.072	888	0.002
Water Renewal Time (*yr*)	4.7		4.0		7.2		5.5	

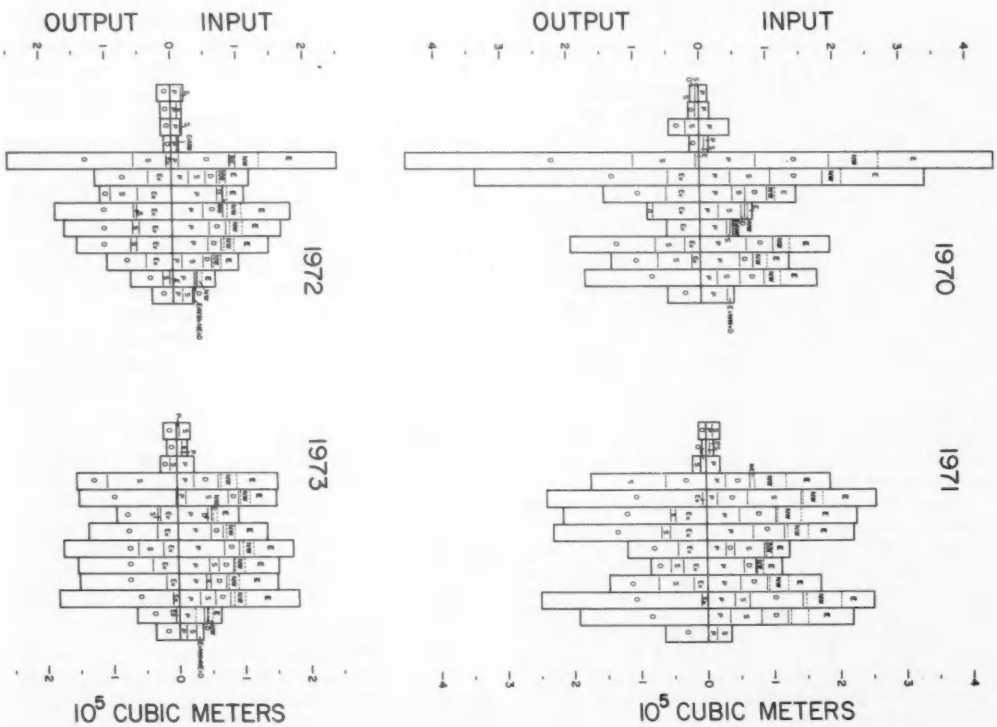

FIG. 3. Seasonal water budgets for the Rawson Lake system in 1970–73, showing the water budgets in different years. Bars represent inputs and outputs for 13 equal 4-wk periods. The inflow bar is divided into portions representing the three subbasins by dashed lines. The small unlabelled portion of some bars is for the NE subbasin. In 1970, the NE subbasin is included in the direct runoff rather than the inflow component because stream records were not available. P = precipitation, E = east inflow, NW = northwest inflow, NE = northeast inflow, D = direct runoff, O = outflow, Ev = evaporation, S = storage.

TABLE 3. Chemical Budget for terrestrial drainage to Rawson Lake, 1970–72. C, N, and P are total values, while other analyses are the dissolved fraction only. (+) indicates net gain; (−) indicates net loss.

Element	Year	Atmospheric input (kg/yr)	Lost to lake (kg/yr)	Retention (+) or net weathering (−) (kg/yr)	% retention of inflow	Atmospheric input (kg/ha per yr)	Outflow (kg/ha per yr)	Retention (+) or net weathering (−) (kg/ha per yr)
P	1970	101.02	17.85	83.17	82	0.29	0.05	0.24
	1971	180.14	23.63	156.51	87	0.53	0.07	0.46
	1972	82.99	15.84	67.15	81	0.24	0.05	0.19
	1973	83.13	11.94	71.19	86	0.24	0.03	0.21
N	1970	1,954.3	350.2	1,604.1	82	5.71	1.02	4.69
	1971	2,504.1	397.1	2,107.0	84	7.32	1.16	6.16
	1972	2,460	233.7	2,226.3	90	7.19	0.68	6.51
	1973	1,632	309.1	1,322.9	81	4.77	0.90	3.87
C	1971	15,096	22,976	−7,880	−52	44.1	67.2	−23.1
	1972	10,737	16,144	−5,407	−50	26.6	47.2	−20.6
	1973	21,808	17,894	3,914	18	63.7	52.3	11.4
H^+	1970	40.88*	4.98	35.90	88	0.120	0.014	0.105
	1971	—	3.09	—	—	—	0.009	—
	1972	—	2.84	—	—	—	0.008	—
	1973	27.15	2.64	24.51	90	0.079	0.008	0.071
Ca	1970	1,787	2,227	−440	−25	5.22	6.51	−1.29
	1971	1,137	2,680	−1,543	−136	3.32	7.83	−4.51
	1972	959	1,272	−313	−33	2.80	3.72	−0.92
	1973	—	2,017	—	—	—	5.90	—
Mg	1970	306	948	−642	−210	0.89	2.77	−1.88
	1971	346	1,012	−666	−192	1.01	2.96	−1.95
	1972	303	499	−196	−65	0.89	1.46	−0.57
	1973	—	754	—	—	—	2.20	—
Na	1970	718	1,417	−699	−97	2.10	4.14	−2.04
	1971	627	1,588	−961	−153	1.83	4.64	−2.81
	1972	309	743	−434	−141	0.90	2.17	−1.27
	1973	532	1,275	−743	−140	1.56	3.72	−2.17
K	1970	553	506	47	9	1.62	1.48	0.14
	1971	342	525	−183	−53	1.00	1.53	−0.53
	1972	231	245	−14	−6	0.68	0.72	−0.04
	1973	—	390	—	—	—	1.14	—
Si	1970	64	5,063	4,999	−7,811	0.19	14.80	−14.61
	1971	1,302	5,374	−4,072	−313	3.81	15.71	−11.90
	1972	80	2,796	−2,716	−3,395	0.23	8.17	−7.94
	1973	104	4,992	−4,888	−4,700	0.30	14.59	−14.29
Cl	1971	772	358	414	54	2.26	1.05	1.21
	1972	687	151	536	78	2.01	0.44	1.57
	1973	1,278	—	—	—	3.74	—	—
SO_4-S	1972	1,034	1,084	−50	−5	3.02	3.17	−0.15
	1973	1,233	—	—	—	3.60	—	—
Fe	1972	—	327.7	—	—	—	0.96	—
	1973	—	374.3	—	—	—	1.09	—

*Based on average pH in 1973.

(J. Cherry, Waterloo University, personal communication; see also Bottomley [1974] and Kennedy [1974]).

ANNUAL INPUT OF ELEMENTS VIA PRECIPITATION

Practically all of the P and N received by terrestrial and aquatic ecosystems at ELA originates from the atmosphere. Precipitation furnishes 0.24–0.53 kg P/ha and 4.77–7.32 kg N/ha annually. Precipitation is assumed to be the sole source of P, because apatite ($Ca_4(PO_4)_3OH$) and other typical mineralogical sources of phosphate have not been observed in the watershed. Fixation of atmospheric N_2 may be an important additional N source for terrestrial systems, but is negligible in natural lakes of the area. Brouzes et al. (1969) found that soils from Quebec black spruce stands fixed 0.97–18.0 kg N/ha per yr, suggesting that N_2 fixation may be a significant N source for boreal watersheds. No studies of terrestrial N_2 fixation have been done at ELA.

Annual carbon input from precipitation was 27–64 kg/ha. This is likely to be a small fraction of CO_2 fixed photosynthetically by terrestrial plants, which probably amounted to at least 4,000 kg/ha annually (Whittaker 1970). On the other hand, it is significant compared to the aquatic primary production, which in Rawson Lake is about 200 kg/ha for phytoplankton (E. J. Fee unpublished data) and 8 kg/ha for periphyton (Schindler et al. 1973a).

Amounts of Ca^{2+}, Mg^{2+}, Na^+, K^+, Cl^-, and SO_4^{2-} found in precipitation, while not high, were a significant contribution when compared with weathering data for the watersheds (Tables 3–6). This will be discussed in more detail below. Undetectable silica was usually found in precipitation.

The concentrations of ions in rainfall varied greatly during the 4 yr of study (Table 7). Mean concentrations and total input of most elements in the highest year were about 2 times those in the lowest year (Tables 3–7). Likens and Bormann (1974) reported similar results. It is thus clearly important to collect several years data to

TABLE 4. Chemical budget for the E subbasin, 1970–73. (+) indicates net gain; (−), net loss.

Element	Year	Atmospheric input (kg/yr)	Outflow (kg/yr)	Retention (+) or net weathering (−) (kg/yr)	% retention of inflow	Atmospheric input (kg/ha per yr)	Lost (kg/ha per yr)	Retention (+) or net weathering (−) (kg/ha per yr)
P	1970	50.27	8.64	41.63	83	0.29	0.05	0.24
	1971	89.81	11.23	78.58	87	0.53	0.07	0.46
	1972	41.41	8.64	32.77	79	0.24	0.05	0.19
	1973	40.90	7.13	33.77	83	0.24	0.04	0.20
N	1970	973.5	173.9	799.6	82	5.71	1.02	4.69
	1971	1,247.2	180.3	1,066.9	86	7.32	1.06	6.26
	1972	1,225.4	174.4	1,051.0	86	7.19	1.02	6.17
	1973	811.7	164.7	647.0	80	4.76	0.97	3.79
C	1971	7,500	10,273	−2,773	−47	44.0	60.3	−16.3
	1972	5,335	7,763	−2,428	−46	31.3	45.6	−14.3
	1973	10,864	9,131	1,733	2	63.8	53.6	10.2
H^+	1970	20.36[a]	1.49	18.87	93	0.120	0.0087	0.111
	1971	—	0.43	—	—	—	0.0025	—
	1972	—	0.38	—	—	—	0.0022	—
	1973	13.53	0.24	13.29	98	0.079	0.0014	0.078
Ca	1970	890	1,261	−371	−42	5.22	7.39	−2.17
	1971	566	1,414	−848	−149	3.32	8.30	−4.98
	1972	477	1,047	−570	−119	2.80	6.14	−3.34
	1973	—	1,212	—	—	—	7.11	—
Mg	1970	153	510	−357	−233	0.90	2.99	−2.09
	1971	172	515	−343	−199	1.01	3.02	−2.01
	1972	152	398	−246	−162	0.89	2.34	−1.45
	1973	—	440	—	—	—	2.58	—
Na	1970	358	772	−414	−116	2.10	4.53	−2.43
	1971	312	832	−520	−166	1.83	4.88	−3.05
	1972	153	604	−451	−295	0.90	3.54	−2.64
	1973	245	756	−511	−209	1.44	4.44	−3.00
K	1970	276	302	−26	−9	1.62	1.77	−0.15
	1971	170	275	−105	−62	1.00	1.61	−0.61
	1972	116	197	−81	−70	0.68	1.16	−0.48
	1973	—	241	—	—	—	1.41	—
Si	1970	32	2,751	−2,719	−8,497	0.19	16.14	−15.95
	1971	649	2,672	−2,023	−312	3.81	15.68	−11.87
	1972	39	2,183	−2,144	−5,500	0.23	12.81	−12.58
	1973	52	2,793	−2,741	−5,271	0.31	16.39	−16.08
Cl	1971	385	197	188	49	2.26	1.16	1.10
	1972	343	81	262	76	2.01	0.48	1.53
	1973	637	—	—	—	3.74	—	—
SO_4-S	1972	515	569	−54	−10	3.02	3.34	−0.32
	1973	614	—	—	—	3.60	—	—
Fe	1972	—	184.6	—	—	—	1.08	—
	1973	—	213.8	—	—	—	1.25	—

[a]Based on 1973 data.

properly characterize nutrient inputs to an ecosystem.

It is usually assumed that rainwater from "natural" areas should have a pH of 5.5–6.0, and that it should be a weak solution of H_2CO_3. Yet in the 2 yr when comprehensive studies of pH were done, 1970 and 1973, the mean annual pH (weighted for amount of rainfall) was 4.94 and 4.98, respectively. Sulfate is the dominant anion in ELA rain. It represents as high a proportion of total anions as it does in culturally polluted areas of the eastern U.S. (see Likens et al. 1972). Total ionic contribution from precipitation is, however, much higher at the U.S. sites. Odors from a small pulp mill at Dryden, Ontario, 65 km to the northeast can occasionally be detected when surface winds are from that direction, so that there may be some local influence. This possibility is now under investigation.

CHEMICAL BUDGETS FOR THE TERRESTRIAL WATERSHED

All portions of the terrestrial watershed had high retentions of P and N, averaging 84% for both elements in all basins and years (Tables 3–6). This result is not surprising in view of the high requirements of vegetation for these elements and the high affinity of soils for PO_4^{2-} (MacLean and MacDonald 1973).

The runoff of P is probably of most interest to aquatic scientists because of its critical role in eutrophication (Vollenweider 1968, Schindler 1974). Dillon and Kirchner (1975) found that forested land on Precambrian substrates in eastern Ontario lost 0.007–0.088 kg P/ha. Our overall average for 4 yr was 0.05 kg/ha, about the middle of their range. Extreme values (all subbasins and years) were 0.02 kg/ha, for the E and NE subbasin in 1974 to 0.110 kg/ha, for the NE subbasin in 1971. Dillon and Kirchner (1975) found an overall average of 0.042 kg/ha exported from other forested igneous watersheds.

Carbon output from terrestrial areas exceeded input from precipitation (Tables 3–6). However, in view of the large amounts of this element removed from the atmosphere by photosynthesis, as mentioned above, actual retention as a proportion

TABLE 5. Chemical budget for the NW subbasin, 1970–73. (+) indicates net gain; (−), net loss.

Element	Year	Atmospheric input (kg/yr)	Outflow (kg/yr)	Retention (+) or net weathering (−) (kg/yr)	% retention of inflow	Atmospheric input (kg/ha per yr)	Lost (kg/ha per yr)	Retention (+) or net weathering (−) (kg/ha per yr)
P	1970	18.53	3.50	15.03	81	0.29	0.06	0.23
	1971	33.30	4.51	28.79	86	0.53	0.07	0.46
	1972	15.08	1.58	13.50	90	0.24	0.03	0.21
	1973	15.27	1.17	14.10	92	0.24	0.02	0.22
N	1970	358.8	64.3	294.5	82	5.71	1.02	4.69
	1971	460.0	85.5	374.5	81	7.32	1.36	5.96
	1972	451.8	44.2	407.6	90	7.19	0.70	6.49
	1973	299.5	38.0	261.5	87	4.77	0.60	4.17
C	1971	2,772	4,834	−2,062	−74	44.1	91.7	−47.6
	1972	1,671	2,920	−1,249	−75	26.6	46.5	−19.9
	1973	4,005	2,228	1,777	44	63.7	35.5	28.2
H^+	1970	7.51	1.90	5.61	75	0.120	0.030	0.090
	1971	—	1.06	—	—	—	0.017	—
	1972	—	0.85	—	—	—	0.014	—
	1973	4.99	0.687	4.30	86	0.079	0.011	0.068
Ca	1970	328	254	74	23	5.22	4.04	1.18
	1971	209	433	−224	−107	3.33	6.89	−3.56
	1972	176	188	−12	−7	2.80	2.99	−0.19
	1973	—	166	—	—	—	2.64	—
Mg	1970	56	135	−79	−141	0.89	2.15	−1.26
	1971	63	179	−116	−184	1.00	2.85	−1.85
	1972	56	84	−28	−50	0.89	1.34	−0.45
	1973	—	74	—	—	—	1.18	—
Na	1970	132	192	−60	−45	2.10	3.06	−0.96
	1971	115	257	−142	−123	1.83	4.09	−2.26
	1972	57	107	−50	−88	0.91	1.70	−0.79
	1973	90	112	−22	−24	1.43	1.78	−0.35
K	1970	102	42	60	59	1.62	0.67	0.95
	1971	63	72	−9	−14	1.00	1.15	−0.15
	1972	43	32	11	26	0.68	0.51	0.17
	1973	—	23	—	—	—	0.37	—
Si	1970	12	693	−681	−5,675	0.19	11.03	−10.84
	1971	239	994	−755	−316	3.80	15.82	−12.02
	1972	14	488	−474	−3,386	0.22	7.77	−7.55
	1973	19	553	−534	−2,811	0.30	8.80	−8.50
Cl	1971	142	46	96	68	2.26	0.73	1.53
	1972	126	19	107	85	2.01	0.30	1.71
	1973	235	—	—	—	3.74	—	—
SO_4-S	1972	190	153	37	19	3.02	2.43	0.59
	1973	226	—	—	—	3.60	—	—
Fe	1972	—	37.3	—	—	—	0.59	—
	1973	—	36.4	—	—	—	0.58	—

[a]Based on 1973 pH data.

of total input is undoubtedly as high as for P and N.

Most of the H^+ entering with rain was retained by the terrestrial areas. This is not surprising, since weathering of feldspars, plagioclases and clay minerals requires substitution of H^+ for major cations (Fisher et al. 1968, Brunskill et al. 1971). As a result of this process, outputs of Ca^{2+}, Mg^{2+}, Na^+, K^+, and Fe from the watershed would be expected to exceed inputs. Reuss (1975) discusses the problem in detail, concluding that consideration of terrestrial systems by simply looking at inputs and outputs of H^+ ions is too simplistic. This is true, except in the case of K, which is not lost to the same extent as other ions (Tables 3–6). There are a number of possible explanations for this. First, watershed minerals containing Na and Ca tend to be more soluble than those containing K (i.e. K is selectively retained in relation to Na [Harris and Adams 1966]). In particular, illite, which is found in soils and overburden of the area (Brunskill et al. 1971) is known to have a high affinity for K (Powers 1959). Brunskill et al. (1971, tables 1 and 2) also found that the surface sediment of Rawson Lake was greatly impoverished in K with respect to local bedrock and terrestrial overburden, which indicates that the element is selectively removed from weathered material somewhere between leaving its original site in bedrock or overburden and reaching the lake bottom. Studies of boreal forest vegetation by Weetman and Webber (1971) have shown that K deficiency occurs frequently in the Canadian Shield, and that 7–15 kg/ha of this element may be removed from soils annually by the biota, possibly accounting for the low losses from the watershed. Likens et al. (1967) also noted lower losses of K via runoff than would be expected from weathering in the absence of biological effects.

Sulfate and chloride also appeared to be supplied almost entirely by the atmosphere. Since their content in local rock is negligible (Brunskill et al. 1971), weathering cannot have contributed significant amounts of either ion (Tables 3–6).

Based on the theory and applications of several workers, Brunskill et al. (1971) predicted that weathering of minerals at ELA would produce an

TABLE 6. Chemical budget for the NE subbasin, 1971–73. (+) indicates net gain; (−), net loss.

Element	Year	Atmospheric input (kg/yr)	Outflow (kg/yr)	Retention (+) or net weathering (−) (kg/yr)	% retention of inflow	Atmospheric input (kg/ha per yr)	Lost (kg/ha per yr)	Retention (+) or net weathering (−) (kg/ha per yr)
P	1971	5.03	1.02	4.01	80	0.53	0.11	0.42
	1972	2.31	0.92	1.39	60	0.24	0.10	0.14
	1973	2.31	0.17	2.14	93	0.24	0.02	0.22
	1971	69.5	15.8	53.7	77	7.32	1.66	5.66
	1972	68.3	15.1	53.2	78	7.19	1.59	5.60
	1973	45.3	16.6	28.7	63	4.77	1.75	3.02
C	1971	419	1,188	−769	−183	44.1	125.1	−81.0
	1972	298	767	−469	−157	31.4	80.7	−49.3
	1973	606	1,338	−732	−121	63.8	140.8	77.0
H^+	1971	—	0.67	—	—	—	0.070	—
	1972	—	0.70	—	—	—	0.073	—
	1973	0.75	0.945	−0.19	−25	0.079	0.099	−0.020
Ca	1971	32	54	−22	−69	3.37	5.68	−2.31
	1972	27	37	−10	−37	2.84	3.89	−1.05
	1973	—	53	—	—	—	5.58	—
Mg	1971	10	24	−14	−140	1.05	2.53	−1.48
	1972	8	17	−9	−113	0.84	1.79	−0.95
	1973	—	21	—	—	—	2.21	—
Na	1971	17	37	−20	−118	1.79	3.89	−2.10
	1972	9	32	−23	−256	0.95	3.37	−2.42
	1973	14	37	—	—	—	3.89	—
K	1971	10	25	−15	−150	1.05	2.63	−1.58
	1972	6	16	−10	−167	0.63	1.68	−1.05
	1973	—	13	—	—	—	1.37	—
Si	1971	36	145	−109	−303	3.79	15.26	−11.47
	1972	2	125	−123	−6,150	0.21	13.16	−12.95
	1973	3	196	−193	−6,433	0.32	20.63	−20.32
Cl	1971	21	11	10	48	2.21	1.16	1.05
	1972	19	7	12	63	2.00	0.74	1.26
	1973	36	—	—	—	3.79	—	—
SO_4-S	1972	29	47	−18	−62	3.05	4.95	−1.90
	1973	34	—	—	—	3.61	—	—
Fe	1972	—	10.5	—	—	—	1.11	—
	1973	—	15.4	—	—	—	1.62	—

TABLE 7. Average concentrations ($C_{\bar{x}}$) of various substances in ELA bulk precipitation. All values are in milligrams per liter except conductivity, which is in mhos per centimeter at 25 C.

	1970	1971	1972	1973	$\bar{x}$	Range
susp. P	0.017	0.017	0.015	0.016	0.016	0.001–0.852
TDP	0.013	0.048	0.020	0.017	0.024	0.001–0.632
ΣP	0.030	0.065	0.035	0.033	0.040	
NH_3-N	0.232	0.215	0.518	0.208	0.293	0–4.350
NO_3-N	0.228	0.210	0.392	0.206	0.259	0.001–2.385
TDN	0.415	0.743	0.929	0.479	0.642	0.031–4.496
susp. N	0.174	0.165	0.088	0.150	0.144	0.001–4.203
ΣN	0.589	0.908	1.017	0.629	0.786	
DIC	0.493	—	—	0.417	0.455	0–0.840
DOC	—	3.321	2.533	5.392	3.749	0.018–24.600
susp. C	1.364	1.561	1.231	2.753	1.727	0.043–31.610
ΣC	—	—	—	8.421	5.860	
Si	0.018	0.024[a]	0.033	0.040	0.029	0–0.162
Ca	0.539	0.412	0.397	—	0.449	0.00–2.08
Mg	0.092	0.125	0.125	—	0.114	0.00–0.78
Na	0.216	0.227	0.128	0.190	0.190	0.00–1.75
K	0.167	0.124	0.096	—	0.129	0.01–1.02
SO_4-S	—	1.686	1.204	1.428	1.439	0.60–50.4
Cl	—	0.280	0.284	0.494	0.353	0.00–2.60
H^+	0.0111	—	—	0.0105	0.0109	0.00005–0.05248
Cond	14.2	—	—	11.3	12.7	3.0–33.0

[a]Omitting three samples which were apparently contaminated.

TABLE 8. Annual losses of cations and anions from the terrestrial watershed of Rawson Lake, millimoles. Net losses (= outflow minus atmospheric input).

	Ca	Mg	Na	K	Σ cation	Si
1970	11	26	30	−1	66	175
1971	38	27	42	5	112	142
1972	8	8	19	0	35	95
	57	61	91	4	$\bar{x}$ 71	137

average of 1 mol of Si/mol of $\Sigma(Ca + Mg + Na + K)$. Net mass balance (i.e. moles in outflow solution minus moles entering as precipitation) for all parts of the terrestrial watershed indicate that the net dissolved material released is deficient in cations to balance with Si (Table 8). One might deduce that chemical weathering according to equations 3 and 5 in Brunskill et al. 1971 is predominant.

CHEMICAL BUDGETS FOR RAWSON LAKE

Inputs of P were 0.05–0.10 g/m² of lake surface per yr. The amount did not appear to be related to total precipitation. About half the input came from streamflow and about half directly from the atmosphere (Table 9).

Nitrogen input ranged from 1.0 to 1.5 g/m² per yr. Again, streams and precipitation furnished roughly equal amounts. Fixation of atmospheric N_2 by aquatic flora is unlikely to be a significant input, based on results from experiments in other lakes in the area (R. Flett personal communication). On the basis of mean depth and inputs of P and N, the lake would be oligotrophic to low mesotrophic in character. Plankton standing crop and production confirms this interpretation (Schindler and Holmgren 1971; Schindler 1972; D. Schindler and E. Fee unpublished data).

As expected for elements that are in great demand by aquatic plants, inputs of P and N to the lake greatly exceeded outflow. Annual retention figures are 51–79%, in the range expected with relatively low rates of water renewal (Vollenweider 1968; Dillon and Kirchner 1975).

Inputs of C also greatly exceeded outputs. Almost all of the entering C was from streamflow, chiefly as dissolved organic compounds. Some C may have left the lake by atmospheric exchange, because epilimnetic partial pressure of CO_2 gas (P_{CO_2}) was always at or above saturation with respect to the atmosphere. Gas exchange experiments using Rn-222 (S. Emerson unpublished data) indicate that this source of error in outflow of C is probably slight, and primary production studies indicate that virtually all of the observed C retention can be accounted for by photosynthetic activity of phytoplankton (Schindler et al. 1973a; E. Fee unpublished data).

The main source of Si was also streamflow. Retention in the lake, while lower than for the above elements, is about half of input. Uptake by diatoms is probably responsible.

Moderate to low retention of Cl^-, SO_4^{2-}, and Na^+ were observed (Table 10). Streamflow was the chief source of all three.

Highly variable retentions were observed for Ca^{2+}, Mg^{2+}, and K^+. The reasons for this are not clear at present, although Lerman and Brunskill (1971) predicted that small amounts of these and other elements should enter the lake from sediment interstitial water.

The mechanism of which a lake retains biologically reactive elements like C, N, and Si is extremely simple. The elements supplied by inflows are assimilated by plankton in the epilimnion of the lake during the period of thermal stratification. These plankton sink slowly through the thermocline (Figure 4), carrying assimilated nutrients with them. Because water below the thermocline is not discharged from the lake via the outlet, outflowing water tends to contain less of the elements than inflowing water during most of spring, summer, and fall. Seasonal isopleths for biologically important elements show this process clearly (for example Fig. 4).

On the other hand, most other elements, which are not removed from the epilimnion by plankton to any significant degree, tend to have outflows roughly equal to inputs.

RELATIONSHIPS BETWEEN CHEMICAL CONCENTRATION AND FLOW

Concentrations of several ions showed some relationships to stream flow, as revealed by simple regression analyses. Total dissolved N, Na, K, Ca, Mg, Si and total C were inversely correlated with flow in the majority of years and basins. This is undoubtedly because rapid subsurface flow during wet periods allows less contact time

TABLE 9. Chemical budget for Rawson Lake, 1970–73. Area of the lake is 54.28 ha. Terrestrial area is 342.09 ha. All data are in kilograms per year; negl. = negligible.

Element	Year	Precip.	NW inflow	E inflow	Other inflow	Total terres. inflow	Total input	Outflow	Retention	% retention of inflow
P	1970	16.01	3.50	8.64	12.71	17.85	33.86	9.59	24.27	72
	1971	28.61	4.51	11.23	7.89	23.63	52.24	17.43	34.81	67
	1972	13.19	1.58	8.64	5.05	15.71	28.90	6.14	22.76	79
	1973	13.19	1.17	7.13	3.64	11.94	25.13	6.11	19.02	76
N	1970	309.9	64.3	173.9	112.0	350.2	660.1	252.4	407.7	62
	1971	397.3	85.5	180.3	131.3	397.1	794.4	385.5	409.9	51
	1972	390.3	44.2	174.4	110.9	329.5	719.8	203.7	516.1	72
	1973	258.7	38.0	164.7	106.4	309.1	567.8	259.0	308.8	54
C	1971	2,395	4,834	12,073	7,869	22,976	25,371	13,897	11,474	45
	1972	1,440	2,920	7,763	5,461	16,144	17,592	6,546	11,046	63
	1973	3,461	2,228	9,131	6,535	17,894	21,355	9,779	11,576	54
H^+	1970	3.75[a]	1.90	1.49	1.59	4.98	8.73	0.336	8.45	97
	1971	3.12[a]	1.06	0.43	1.60	3.09	6.21	0.377	5.92	95
	1972	2.73[a]	0.85	0.38	1.61	2.84	5.57	0.197	5.42	97
	1973	4.33	0.69	0.24	1.72	2.65		0.157		
Ca	1970	83	254	1,261	712	2,227	2,510	1,513	997	40
	1971	180	433	1,414	833	2,680	2,860	3,191	−331	−12
	1972	152	188	1,047	559	1,794	1,946	1,873	73	4
	1973	205[b]	166	1,212	639	2,017	2,222	2,389	−167	−8
Mg	1970	49	135	510	303	948	997	746	251	25
	1971	55	179	515	318	1,012	1,066	1,128	−61	−6
	1972	48	84	398	222	704	752	670	82	11
	1973	51[b]	74	440	240	754	805	783	22	3
Na	1970	114	192	772	453	1,417	1,531	1,172	359	23
	1971	100	257	832	499	1,588	1,688	1,474	214	13
	1972	49	107	604	337	1,048	1,097	912	185	18
	1973	78	112	756	407	1,275	1,353	1,141	212	16
K	1970	7	42	302	162	506	593	291	302	51
	1971	54	72	275	178	525	579	610	−31	−5
	1972	37	32	197	116	345	382	340	42	11
	1973	59[b]	23	241	126	390	449	494	−45	−10
Si	1970	10	693	2,751	1,619	5,063	5,073	2,955	2,188	42
	1971	206	944	2,672	1,708	5,374	5,580	3,295	2,285	41
	1972	12	488	2,183	1,271	3,942	3,954	2,146	1,808	46
	1973	16	553	2,793	1,646	4,992	5,008	2,681	2,327	46
Cl	1971	123	46	197	115	358	481	380	101	21
	1972	109	19	81	51	151	260	183	78	30
	1973	202	—	—	—	—	—	—	—	—
SO_4-S	1972	164	153	569	362	1,084	1.248	993	255	20
	1973	196	—	—	—	—	—	—	—	—
Fe	1972	negl.	37.5	184.6	105.8	327.9	327.9	40.8	287.1	88
	1973	negl.	36.4	213.8	124.1	374.3	374.3	61.6	312.7	84

[a]Based on 1973 data.
[b]No data. Mean of 1970–72 precipitation values.

TABLE 10. Inputs (I), outflows (O), and net losses or gains (N) of elements from four small forested watersheds. All data are in kilograms per hectare per year. (+) indicates net gain; (−), net loss; negl. = negligible.

	Clear Lake, Ont.[a]			Hubbard Brook, N. H.[b,c]			H. A. Andrews experimental Forest, Oreg.[d]			Rawson Lake, Ont.			Yr data
	I	O	N	I	O	N	I	O	N	I	O	N	
Ca	14.12	6.75	+7.37	2.3	12.5	−10.2	4.99	51.98	−46.99	3.78	6.02	−2.24	3
Mg	5.40	2.33	+3.07	0.6	2.9	−2.3	1.02	12.57	−11.55	0.93	2.40	−1.47	3
Na	1.28	1.58	−0.30	1.6	6.8	−5.2	1.75	29.69	−27.94	1.60	3.67	−2.07	4
K	0.96	0.82	+0.14	0.9	1.7	−0.8	0.19	1.74	−1.55	1.10	1.24	−0.14	3
ΣP	0.352	0.088	+0.264	0.11	0.01	0.10	0.27	0.52	−0.25	0.32	0.05	+0.27	4
ΣN	9.95	1.26[e]	+8.69	6.5	1.6	+4.9[b]	0.99	0.48	+0.41	6.35	0.94	+5.31	4
Si	2.66	3.85	−1.19	negl.	16.4	−16.4	negl.	99.3	−99.3	1.13	13.32	−12.19	4
SO_4-S	—	—	—	11.9	16.2	−4.3	—	—	—	3.02	3.17	−0.15	1
Cl	—	—	—	6.3	4.6	+1.7	—	—	—	2.14	0.74	+1.40	1
Fe	—	—	—	—	—	—	—	—	—	negl.	1.03	−1.03	2

[a]Schindler and Nighswander 1970, table 6.
[b]Likens et al. 1970, table 5.
[c]Likens and Bormann 1974.
[d]Fredriksen 1972, table 2.
[e]Inorganic N only.

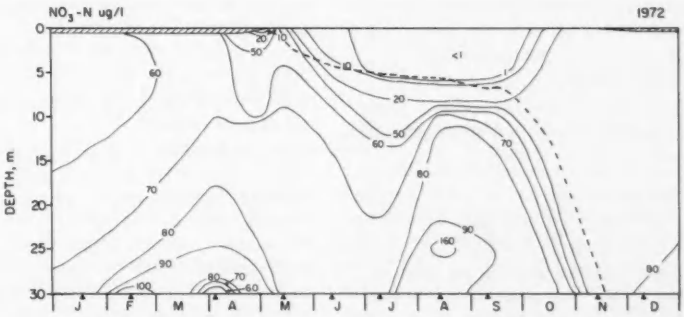

FIG. 4. Nitrate nitrogen, an example of a chemical species that is efficiently retained by the lake due to uptake by plankton and sedimentation through the thermocline. The position of the thermocline is shown by a dotted line.

between water and geologic materials. The slope of the relationships was always small so that the seasonal distribution of nutrient losses is similar to the seasonal hydrograph. For example, in the NW subbasin, Na and Si concentrations decreased only 0.024 and 0.092 g/m³ for each cubic meter increase in flow, respectively. Little or no correlation with flow was observed for Cl, SO_4, total P, or conductivity. The only ion with output directly related to flow was H^+, which was positively correlated only in 1 yr. These results agree well with those obtained at Hubbard Brook (Johnson et al. 1968), although K and NO_3 are more complicated at the latter site, reflecting periods of biological activity.

EFFECT OF THE 1973 WINDSTORM

Although it does not appear in this analysis, a severe windstorm on June 26, 1973 blew down a high percentage of the trees in the basin, causing increased losses of several elements. This effect is "masked" in the 1973 figures given here by the fact that the highest portion of the annual outflow occurred before the windstorm. A detailed analysis will be presented in a later publication.

General Discussion

Annual inputs of N and P to terrestrial areas are much smaller than rates of uptake by boreal black spruce, red spruce, and balsam found by Weetman and Webber (1971). While terrestrial N_2 fixation is unknown in the area, forest growth in the Rawson Lake Watershed may be limited by availability of these elements. Rennie (1955), in a study of forest growth, found that pine and mixed conifers required 50 and 100 kg/ha of P respectively, for 100 yr of forest growth. At average retention rates of P in the Rawson Lake watershed, this amount would require 150–300 yr

to supply. Clear-cutting procedures remove approximately 50–60% of the forest biomass, and although trunk wood has a low nutrient content relative to leaves and twigs, quantities of these elements removed may be large enough to cause P deficiency by second-growth vegetation. Likens and Bormann (1974) also documented large N losses due to clear-cutting in the White Mountains of New Hampshire. Stream runoff and removal of biomass were about equally responsible.

Losses of all elements from the Rawson Lake watershed are similar to Clear Lake, also in the Canadian Shield, but lower than Hubbard Brook, underlain by quartz, plagioclase, and biotite, or the H. A. Andrews Experimental Forest of western Oregon (Table 10), demonstrating the extremely low solubility of Precambrian bedrock and overburden. The Andrews Experimental Forest, which receives twice the precipitation of other areas and is underlain by much more soluble bedrock, lost many times more Na, K, Ca, and Mg than other systems.

Year-to-Year and Subbasin to Subbasin Differences in Chemical Yield

Great year-to-year variations (at least 2 times) in inputs and outflows of all elements were found within a single watershed at Hubbard Brook and the Andrews Experimental Forest, as well as at Rawson Lake (Tables 4–6). This does not appear to be correlated with average annual water yields in significant way. It, therefore, appears impossible to obtain an accurate estimate for the chemical budget of any terrestrial watershed without several years data and directly applied hydrological analysis.

In general, changes in water flow were several orders of magnitude greater than changes in chemical concentration. Therefore, seasonal dynamics of nutrient yields follow the seasonal hydrological regime rather closely (Fig. 3).

There were, however, considerable differences between subbasins in the retention or yield of many chemicals, even within 1 yr (Tables 4–6). The annual yields of Ca, Mg, Na, K, and Si were usually higher in the E subbasin, which is larger and contains a wider variety of physiographic conditions than the others. Mean differences between the highest and lowest basins in any year often exceeded 2x. In contrast, yields and retentions of P and N were remarkably similar for the different basins in a given year. Considerable caution must therefore be exercised in interpreting experimental studies where one watershed is used as a control for another, particularly when budgets for weathering products of the basin are compared. Pretreatment data for control and treatment basins should be obtained whenever possible.

The percentage of incoming P and N retained by both terrestrial and aquatic ecosystems also appeared to be relatively constant (Tables 3 and 9). Because the total input varies greatly from year to year, this consistency must mean that a constant proportion of incoming material is in forms utilizable by biota.

If all inputs and outputs are well known, the ratio of nutrients retained by an ecosystem must reflect the relative demand for them by the system's biota. For example, the inputs to lake 239 contained N and P in an average ratio of 19.5:1 by weight. In outflow, this ratio increased to 29:1, so that the two nutrients were retained by the lake in the ratio 16:1, very near the expected ratio for phytoplankton. If nutrients in the lake are largely affected by biological rather than chemical processes, such an increase in the N:P ratio from input to output must indicate that phosphorus is the most limiting nutrient, on an annual basis.

In comparison, in the terrestrial system the ratios of N:P in nutrient supplied by precipitation, outflowing, and retained by the basin were similar, 19.5, 18.8, and 19.7 to 1, respectively. We cannot correct these figures for N_2 fixation and denitrification by the terrestrial biota, so at present there is no evidence that either of these nutrients is more limiting than the other.

It is obvious from this study and others reviewed that the terrestrial, aquatic, and atmospheric dynamics of several nutrients are interrelated, and in many cases interdependent. The production of an aquatic ecosystem depends to a great degree on its nutrient input (Vollenweider 1968; Schindler and Fee 1974). This fact has been well known for terrestrial ecosystems for some time, based upon our agricultural experience. When one considers the production of an ecosystem, other nutrient cycles or other parts of the biosphere cannot therefore be disregarded. Many examples of the futility of the traditional "closed" approach to ecosystem ecology may be cited. Schindler et al. (1973b) showed that atmospheric input of C to lake 227 allowed it to become eutrophic, in spite of C concentrations that previous authors would have considered too low to allow eutrophication to take place (for example King 1970). The importance of terrestrial management practices to aquatic systems in the same watershed is obvious from the forest work of Likens et al. (op. cit.) as well as that of agricultural watersheds (MacLean and MacDonald 1973). Dillon and colleagues (Dillon

and Kirchner 1975; Rillon and Rigler 1975) have measured the nutrient yield of watersheds on different geological substrates subjected to different management practices and used the results in a scheme for managing eutrophication in Ontario lakes. The ecosystem, considered by most ecologists to be the fundamental ecological unit, is not definable in a way that allows these nutrient processes to be assessed, because there is no easy way of quantifying ecosystem boundaries. The watershed or drainage basin is a much more realistic ecological unit to use when production or other chemically and hydrologically dependent processes are studied.

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Energy Dynamics of Two Benthic Crustaceans in Relation to Diet

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SWISS, J. J., AND M. G. JOHNSON. 1976. Energy dynamics of two benthic crustaceans in relation to diet. J. Fish. Res. Board Can. 33: 2544–2550.

Energy dynamics were studied in *Asellus racovitzai* (Crustacea: Isopoda) and *Gammarus fasciatus* (Crustacea: Amphipoda) fed various selected algal species (Cyanophyta — *Oscillatoria* sp., *Anabaena flos-aquae*, *Anacystis nidulans*, *Microcystis aeruginosa*; Chorophyta — *Chlorella ellipsoidea*, *Scenedesmus dimorphus*, *Ankistrodesmus falcatus*) and lake sediments. Calculations of growth, production, assimilation, and growth efficiency were made from measurements of weight change, respiration rate, and caloric content of experimental animals. Although growth rate, production, and growth efficiency were often highest in animals fed green algae, differences were not attributable solely to green vs. blue-green taxonomic groups. The relationship between assimilation rate and growth efficiency was examined, and the possible consequences of lower values of assimilation were discussed in terms of delayed development to maturity and reproduction.

SWISS, J. J., AND M. G. JOHNSON. 1976. Energy dynamics of two benthic crustaceans in relation to diet. J. Fish. Res. Board Can. 33: 2544–2550.

Nous avons étudié la dynamique de l'énergie chez *Asellus racovitzai* (Crustacea: Isopoda) et *Gammarus fasciatus* (Crustacea: Amphipoda) nourris à diverses espèces d'algues (Cyanophyta — *Oscillatoria* sp., *Anabaena flos-aquae*, *Anacystis nidulans*, *Microcystis aeruginosa*; Chorophyta — *Chlorella ellipsoidea*, *Scenedesmus dimorphus*, *Ankistrodesmus falcatus*) et à des sédiments lacustres. Des mesures de changements de poids, de taux de respiration et de contenu calorique sur des animaux expérimentaux nous ont permis de calculer la croissance, la production et l'efficacité d'assimilation et de croissance. Bien que le taux de croissance, la production et l'efficacité de croissance montrent le plus souvent un maximum chez les animaux nourris aux algues vertes, les différences ne sont pas attribuables seulement aux groupes taxonomiques algues vertes versus algues bleu-vert. Nous analysons la relation entre le taux d'assimilation et l'efficacité de croissance et discutons des conséquences possibles des valeurs inférieures d'assimilation en termes de maturité et de reproduction retardées.

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INCREASES in algal biomass are associated with cultural eutrophication, and members of the phylum Cyanophyta (blue-greens) often dominate, and in some cases, displace other phyla by forming heavy blooms (Arnold 1971). Such shifts in algal community type could conceivably cause alterations in the specific composition of benthic macroinvertebrate communities (Peterka and Knutson 1970; Johnson and Brinkhurst 1971; Beeton and Edmondson 1972). Assimilation and the efficiency of energy storage by certain macroinvertebrate species could be altered markedly because of shifts to algal species of lower nutritional value. Preferences by benthic macroinvertebrates for various algal species have been related to a number of factors including taste, calorific value, presence of inhibiting structures, and presence of toxins (Greze 1968; Paine and Vadas 1969; Hargrave 1970, 1971). With the formation of new communities of algae some or all of the above factors may be altered, and macroinvertebrate species shifts and possibly reduced productivity in the benthic community may occur.

It was the purpose of this study, therefore, to examine differences in energy dynamics of benthic invertebrates attributable to algal food

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sources, with specific reference to members of the phylum Cyanophyta.

Materials and Methods

The crustaceans *Asellus racovitzai* (Isopoda) and *Gammarus fasciatus* (Amphipoda) were collected from Rice Lake in Northumberland County, Ontario (44°10′N, 78°10′W). These organisms were maintained under greenhouse conditions in 80-liter plastic tubs containing natural mud sediments. Temperature was controlled to 18 ± 2 C and the only care required was the occasional addition of water when levels in these containers became low.

Experimental diets consisted of fresh cultured algae (the green algae *Ankistrodesmus falcatus*, *Scenedesmus dimorphus*, and *Chlorella ellipsoidea*; and the blue-green algae *Microcystis aeruginosa*, *Anacystis nidulans*, *Anabaena flos-aquae* and *Oscillatoria* sp., grown in ASM-1 medium), aged cultured algae, and sediments from two stations in the Bay of Quinte, Lake Ontario (eutrophic site in inner Bay and mesotrophic site in outer Bay). The aged algae were produced by seeding aliquots of fresh algae with 0.1 ml of mud to introduce bacteria and incubating in darkness at 18 C for 1 mo.

Caloric values for all diets and experimental organisms were determined using the method of Phillipson (1964). Five species of algae used had mean caloric contents between 5200 and 5400 cal/g dry wt, while *M. aeruginosa* was slightly lower at 5133 cal/g and *Ankistrodesmus falcatus* greater at 5648 cal/g. Significant differences between species were not found. This is not surprising, however, since all algae were grown under identical nutrient and light regimes and therefore probably had similar chemical composition (Parsons et al. 1961).

Equal quantities (equivalent to 20 mg dry wt) of the above diets were mixed with mud that had been heated to 100 C for 5 h to kill macroinvertebrates. These mixtures were placed in 250-ml Erlenmeyer flasks, water was added until the flasks were full, and the contents were allowed to settle for 1–3 h.

Animals were removed from holding tanks and placed in glass bottles without sediment for 24 h to allow for evacuation of their digestive tracts. Groups of 10 immature animals were blotted on paper towels, weighed to ±0.001 mg, and introduced into feeding bottles described above. Immature animals were chosen because they would exhibit higher growth rates than adults, and therefore, any alteration attributable to diet would be more easily detected. Ten groups of animals (10 animals per group) were assigned randomly to each diet and 10 additional groups were weighed, dried at 55 C for 24 h, and reweighed to obtain percent dry biomass. This value was used to calculate the initial dry weights of test animals. Statistical comparison of initial weights indicated that there was no significant difference ($P < .05$) among the mean weights assigned to each treatment.

The feeding bottles were submerged in an aerated darkened water bath maintained at 18 ± 1 C. Aeration in the water bath was sufficiently high to maintain adequate levels of dissolved oxygen in the feeding bottles throughout the experiment. After 18 days, animals were removed from the feeding bottles and counted.

Respiration rates were then determined using a modification of the method of Johnson and Brinkhurst (1971). Animals were placed into 30-ml glass-stoppered bottles containing no substrate and filled with filtered (0.45 μl) water. Dissolved oxygen content was 90% of air saturation. The bottles were incubated at 18 ± 1 C in a darkened water bath for 4–24 h. Oxygen concentrations before and after incubation were measured with a Yellow Springs Instruments oxygen meter and Model 54 B.O.D. probe. The oxygen consumed through respiration was assumed to be the difference between measured oxygen content in control (no animals) and test bottles. The oxycaloric equivalent 3.38 cal/mg O_2 (Ivlev 1934) was used to convert oxygen consumed to energy expended. The animals were then dried, weighed, and frozen until caloric content was measured.

From values of weight change, respiration rate, caloric content, and mortality, the following calculations were made:

i) Percent change in dry weight

$$Pc = \frac{(W_2 - W_1)}{W_1} \times 100$$

where, W_2 = final mean dry weight of animals per bottle in grams; W_1 = initial mean dry weight of animals per bottle in grams.

ii) Relative growth rate

$$G = \frac{(W_2C_2 - W_1C_1)}{(W_1C_1 \times T)} \quad (1)$$

where, C_2 = final caloric value in calories per gram dry weight; C_1 = caloric value (control) in calories per gram dry weight; T = time in days; G = growth rate in calories per calorie per day.

iii) Population production (adapted from Winberg et al. 1971)

$$P = \frac{(N_1 + N_2)}{2} \times \frac{(W_2C_2 - W_1C_1)}{T} \quad (2)$$

where, N_1 = initial number of animals per bottle; N_2 = final number of animals per bottle; P = population production in calories per day.

iv) Population assimilation

$$A = P + R \quad (3)$$

where, P = production, from equation (2); R = respiration rate in calories per day; A = population assimilation in calories per day.

v) Population growth efficiency (Ivlev 1966)

$$K_2 = \frac{P}{A}$$

where, P = production, from equation (2); A = assimilation, from equation (3); K_2 = population growth efficiency.

To determine the possible presence of inhibitory substances released by the algae, the effect of algal filtrates on crustacean respiration rate was determined for filtrates of *Oscillatoria* sp., *Anabena flos-aquae* (both blue-green), and *S. dimorphus* (green). This was done by filtering algal cultures through 0.45 μm filters and exposing *Asellus racovitzai* to the filtrate. Controls were ASM-1 algal growth medium and water.

Results

Crustaceans Fed Fresh Cultured Algae

Relative growth rate (G), population production (P), and population assimilation rates (A) were all highest for *A. racovitzai* fed the green algae *Ankistrodesmus falcatus* (0.076 cal/cal per day, 1.014 cal/day, and 1.487 cal/day, respectively). The next highest rates were observed for *Asellus* fed *S. dimorphus*. Growth rate averaged 0.049 cal/cal per day in these animals, while P and A were 0.678 and 1.061 cal/day, respectively. The lowest rates were observed for *Asellus* fed *M. aeruginosa*, *C. ellipsoidea*, and *Oscillatoria* sp., with intermediate values for those fed *Anabaena flos-aquae* and *Anacystis nidulans* (Fig. 1 and 2). Mortality averaged 27% and varied from about 20% for animals fed *Ankistrodesmus falcatus*, *C. ellipsoidea*, and *Anacystis nidulans* to near 30% for those fed *S. dimorphus* and about 40% for *M. aeruginosa* and *Oscillatoria* sp.

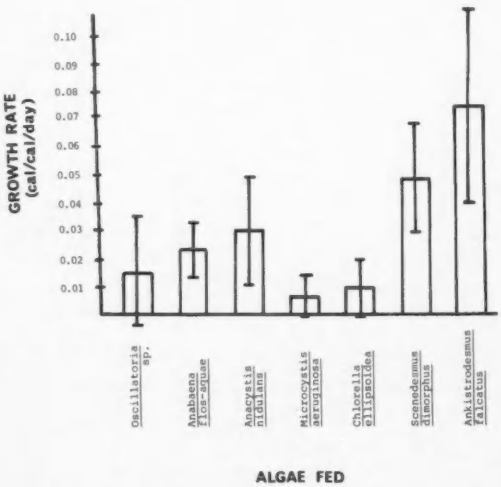

FIG. 1. Relative growth rates (mean ± 1 SD) of *Asellus racovitzai* fed various algae.

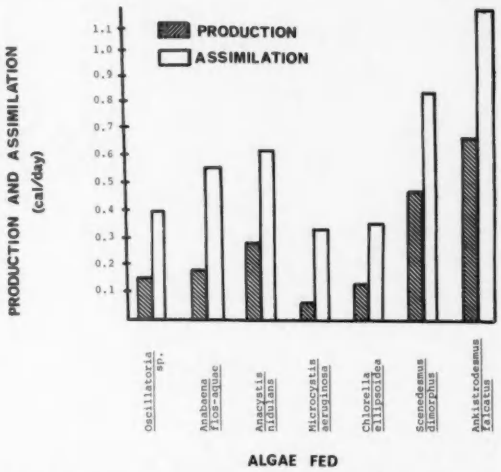

FIG. 2. Population production and assimilation rates of *A. racovitzai* fed various algae.

Growth efficiencies (K_2) were not significantly different for *Asellus* fed *Ankistrodesmus falcatus* (0.66), *S. dimorphus* (0.63), *Anacystis nidulans* (0.51), and *Anabaena flos-aquae* (0.51). Values for animals fed *C. ellipsoidea* (0.36), *M. aeruginosa* (0.20), and *Oscillatoria* sp. (0.35) were significantly lower ($P < 0.05$) than those determined for *Ankistrodesmus* and *Scenedesmus*.

When fresh algae were fed to *G. fasciatus*, the greatest weight changes were again recorded for animals on diets of *A. falcatus* and *S. dimorphus* (69.9% and 117.1%, respectively). Although these weight changes were not significantly different from those observed for animals fed the other algae, the general pattern for *Gammarus* and *Asellus* was similar (Fig. 3).

Crustaceans Fed Aged Cultured Algae

Determinations of rates of energy loss through decomposition, about 0.80%/day at 18 C, showed that all algae lost energy at approximately the same rate ($P < 0.05$). When these "aged" algae were offered to *Asellus racovitzai*, animals fed *Ankistrodesmus falcatus* and *S. dimorphus* (which had yielded the highest rates of G, P, and A in the fresh state) had growth rates that were the same or lower than values calculated for animals fed all other algae (Fig. 4). Growth rates for animals fed *Anabaena flos-aquae* and *C. ellipsoidea* also were reduced after aging. However, when *M. aeruginosa* and *Oscillatoria* sp. were fed, G values were similar to those recorded when these algae were offered fresh. This pattern was also repeated for values of P, A, and K_2.

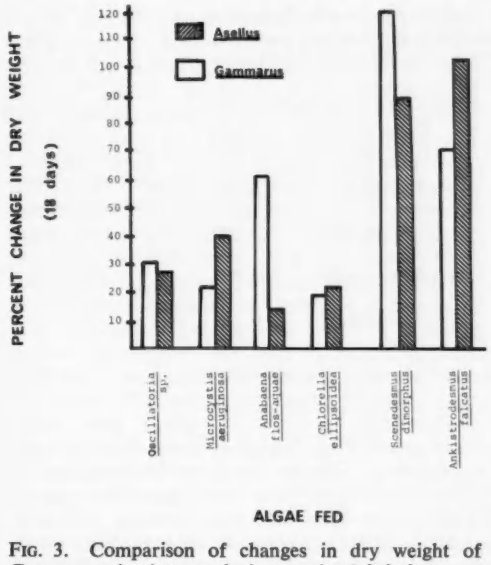

FIG. 3. Comparison of changes in dry weight of *Gammarus fasciatus* and *A. racovitzai* fed the same species of algae.

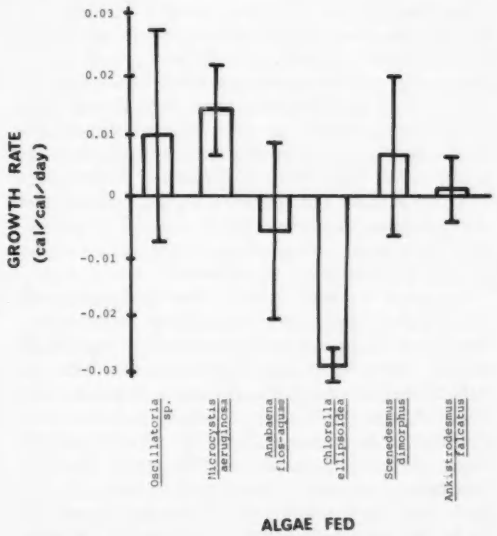

FIG. 4. Relative growth rates (mean ± 1 SD) of *A. racovitzai* fed algae aged in mud for 30 days.

The relationship between assimilation and growth efficiency for *Asellus racovitzai* (Fig. 5) indicates that there is a critical level of assimilation which *Asellus* must maintain to have a high efficiency of energy storage. Above this level,

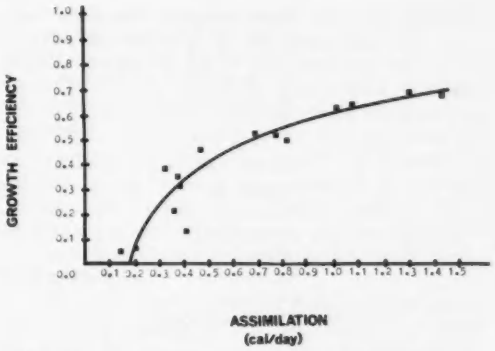

FIG. 5. Assimilation vs. growth efficiency of *A. racovitzai* (curve calculated by method of least squares: $y = -0.289 + 2.10x - 1.83x^2 + 0.60x^3$).

growth efficiency does not change greatly over a wide range in assimilation. Below this level, however, growth efficiency drops off rapidly.

CRUSTACEANS FED NATURAL SUBSTRATES

Muds from the inner and outer reaches of the Bay of Quinte were similar in their ability to support growth in *A. racovitzai*. Although population production and assimilation were higher for *Asellus* fed inner-Bay mud ($P < 0.01$), growth rates and growth efficiencies were similar for animals fed the two diets (Table 1).

RESPIRATION RATES OF CRUSTACEANS IN ALGAL CULTURE FILTRATES

Respiration rates of *A. racovitzai* exposed to algal culture filtrates (respiration measured as milligrams O_2 consumed per gram dry weight per day) were as follows:

	A. racovitzai ($\bar{x}$ + SD)
Well water	17.3 ± 7.2 $N = 10$
ASM-1 media	19.6 ± 5.0 $N = 10$
S. dimorphus	20.1 ± 13.6 $N = 10$
Anabaena flos-aquae	23.8 ± 9.0 $N = 10$
Oscillatoria sp.	26.7 ± 12.2 $N = 10$

Respiration rates of *Asellus racovitzai* were higher in animals exposed to the blue-green algae *Anabaena flos-acquae* and *Oscillatoria* sp. than in those exposed to filtrates of the green algae *Scenedesmus dimorphus*, water, and culture medium controls ($P < 0.05$).

TABLE 1. Growth rate, production assimilation, and growth efficiency of *Asellus racovitzai* fed muds from the inner Bay (Big Bay) and outer Bay (Glenora) of the Bay of Quinte. *P < .01; NS = not significant. N = number of observations.

	Inner Bay ($\bar{x} \pm$ SD)	Outer Bay ($\bar{x} \pm$ SD)	t[a]
Growth rate (*cal/cal per day*)	0.077±0.028 $N = 10$	0.060±0.021 $N = 9$	1.40 NS
Production (*cal/day*)	0.413±0.148 $N = 10$	0.226±0.095 $N = 9$	3.22*
Assimilation (*cal/day*)	0.834±0.222 $N = 10$	0.477±0.150 $N = 9$	4.05*
Growth efficiency	0.489±0.095 $N = 10$	0.452±0.129 $N = 9$	0.72 NS

[a]t-value from Student's t-test for the difference between independent means.

Discussion

This study demonstrates that growth, production, and assimilation rates as well as growth efficiencies in *Asellus* and *Gammarus*, are profoundly affected by the type of algae available as food. Generally, energy use was highest for animals fed green algae (Chlorophyta) and lowest for animals fed blue-green algae (Cyanophyta) with one exception. *Chlorella ellipsoidea*, also a green, consistently produced low values for the above parameters. Other studies also have described deleterious effects of *Chlorella* diets ranging from reduced ingestion rates to shorter life spans for a variety of invertebrates (Arnold 1971; Taub and Dollar 1968). These reports, plus observations made in this study, indicate that the suitability of various algae as food cannot be determined solely on the basis of broad taxonomic groups. Rather, each species must be evaluated separately to determine its capacity for supporting growth and production in animals.

In the present study, growth efficiencies in juvenile *Asellus* fed fresh algae ranged between 20.9 and 66.4%. Other workers using juvenile animals reported growth efficiencies close to those found in this study (Richman 1958; Schroeder 1971; Waldbauer 1967; Johnson and Brinkhurst 1971).

Asellus racovitzai fed the green algae *Ankistrodesmus falcatus* and *S. dimorphus* and those fed the blue-green algae *Anabaena flos-aquae* and *Anacystis nidulans* showed no significant differences in growth efficiency. Rates of growth, production, and assimilation, however, were different for these animals. This observation is supported by Richman (1958) who reported that *Daphnia pulex* had essentially constant growth efficiency at different food intake levels. Therefore, for these *Asellus*, once energy was assimilated, it was used with apparently equal efficiency, in terms of storage of energy as biomass, regardless of source. Because different quantities of energy were assimilated, either these algae were eaten at different rates, or once eaten assimilation rates varied with algal species. This conclusion is supported by Hargrave (1970), who found that *Hyalella azteca* (Amphipoda) fed the blue-green algae *Anabaena* sp. and *Anacystis* sp. had assimilation efficiencies and ingestion rates much lower than those recorded for the same animals fed green algae and diatoms.

Asellus fed *Oscillatoria* sp., *M. aeruginosa*, and *C. ellipsoidea* had growth, production, and assimilation rates that were significantly lower than those of animals fed *Ankistrodesmus falcatus* and *S. dimorphus*. In these cases, however, the reduction may have been of such magnitude that growth efficiency was also affected.

Impaired growth, rather than differences in survival, was the major contributor to low production. Although mortality was higher in animals fed *M. aeruginosa* and *Oscillatoria* sp. than in those fed other algae, the difference in production from *Asellus* fed more suitable diets was accounted for by impaired growth to a much greater extent than by increased mortality (see Fig. 1). The higher mortalities observed in animals fed these two species may be extensions of mechanisms that reduced growth. Animals fed all other species of algae exhibited mortalities very close to mud controls (17.2–28.3%) even though growth and production rates were significantly different, often by an order of magnitude.

Arnold (1971), Hargrave (1970), and McMahon and Rigler (1965) all postulated algal toxins as a possible cause of reduced ingestion

and/or assimilation in their respective experimental animals. In the present study, toxins also may be the primary factor that caused reduced rates of growth, production, and assimilation. Production of toxins by Cyanophyta is well documented (Grant and Hughes 1953; Ingram and Prescott 1954; Hughes et al. 1958; Gorham 1962, 1964), and *Chlorella* may, under certain circumstances, produce toxic materials (McMahon and Rigler 1965). Although it is not possible to rule out some physical factor (e.g. size, shape, cell wall thickness) as the inhibiting agent (Edmondson 1957), this seems doubtful in the present study because algae similar in size and shape caused significantly different rates of growth, production, and assimilation.

The fact that respiration rates of *Asellus* were higher when exposed to filtrates of blue-green algae indicates the presence of some factor, probably chemical, that affected disposition of energy between respiration and growth. The two fresh algae that produced the highest growth rates in *Asellus*, (*Ankistrodesmus falcatus* and *S. dimorphus*) supported much lower rates of growth after aging, as might be expected with all algae with similar rates of decomposition and energy loss. On the other hand, the growth rates of *Asellus* fed aged *Oscillatoria* sp. and *M. aeruginosa* did not change appreciably. During the aging process the algae, which were initially an unsuitable food source, were rendered as suitable as other aged species. The presence of a toxin in the fresh state could have reduced ingestion or assimilation (although other factors such as changes in nonfecal excretion cannot be excluded). Therefore, the reduced capacity of certain algal species to support growth in *A. racovitzai* and *G. fasciatus* seems to be attributable to the presence of some toxin.

The upper Bay of Quinte is characterized by highly productive waters containing a proliferation of blue-green algae (McCombie 1967). Benthic crustaceans, however, are restricted from the inner reaches (Johnson and Brinkhurst 1971). Experiments discussed thus far indicate that the presence of large quantities of blue-green algae in the inner Bay may be inhibitory to crustaceans. But when muds from the inner and outer Bay were fed to *Asellus*, this hypothesis was not supported. In fact, *Asellus* fed muds from the inner Bay assimilated more energy and had higher rates of production than *Asellus* fed outer-Bay muds, although growth efficiencies for animals fed the two muds were the same. The higher assimilation rate of *Asellus* in inner-Bay muds was a result of either increased ingestion or increased assimilation efficiency (assimilation/ingestion). Higher primary productivity in the inner Bay may provide a greater quantity of available digestible material than is found in muds from the less eutrophic outer Bay. Although these experiments with mud diets do not support the hypothesis of toxic effects, the suitability of both muds may be related to the types of algae present in surface sediment and their state of decomposition. Possibly, deleterious effects occur only at the time that senescent blooms are deposited on the bottom sediments.

This study has shown that assimilation rates are related directly to the species of algal food available. If, through the process of eutrophication, dominant algal populations are changed, giving rise to large quantities of algae similar in effects to some of the species studied here, assimilation and efficiency of energy storage in *A. racovitzai* and *G. fasciatus* could be altered markedly.

Some of the growth efficiencies found in this study could be low enough to retard the development time of *A. racovitzai* with significant ecological consequences. "Critically low" growth efficiencies could delay crustacean developmental stages to a point where they no longer coincide with appropriate environmental cycles. Johnson (1970) reported that the lowest value he recorded for a gravid female *Asellus* was 7.70 cal/animal. *Asellus racovitzai* has a life span of 1 yr. Using growth rates determined in this study, and multiplying by 365 days, possible achievable caloric values were obtained for *A. racovitzai* fed the various algae.

Algae fed	Energy accumulated/Y (*cal*)
Ankistrodesmus falcatus	45.2
S. dimorphus	27.1
C. ellipsoidea	5.5
Anacystis nidulans	17.5
Anabaena flos-aquae	13.6
M. aeruginosa	3.6
Oscillatoria sp.	9.4

These values are probably an overestimation because these animals were immature and growing at a greater rate than they would maintain later in their lives. In addition, the temperature used in these experiments (18 ± 1 C) would promote greater growth than would occur in nature, especially during the winter at ambient temperatures of 1–2 C. Comparing these values with Johnson's (1970) figures of 7.70 cal shows that, even with these inflated growth rates, *Asellus* fed *C. ellipsoidea* (5.5 cal/animal) and *M. aeruginosa* (3.6

cal/animal) would not be capable of storing enough energy to produce eggs annually. Therefore, shifts in the dominant algal type could cause a reduction in fecundity (per unit time) in crustacean macroinvertebrates with a subsequent decline of these organisms in the benthic community.

Acknowledgments

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Glomerular Mesangial Fibrosis in Hatchery-Reared Rainbow Trout (*Salmo gairdneri*)

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Light and electron microscopic studies were performed on tissues of hatchery-reared rainbow trout (*Salmo gairdneri*) having a disease of currently unknown etiology with external symptoms of severe edema which causes increased mortality rate. Comparison with unaffected trout tissues revealed loss of cellularity in glomerular tufts with a replacement of mesangial cells by connective tissue. Ultrastructural studies showed the material to be collagen and established the diagnosis of glomerular mesangial fibrosis. The glomerular lesion was associated with alterations in lining epithelium of proximal tubules and extensive debris within tubule lumens. The findings are compared to glomerular lesions in mammalian and amphibian kidney.

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Les auteurs ont étudié au microscope photonique et électronique les tissus de truites arc-en-ciel (*Salmo gairdneri*) d'élevage affectées d'une maladie à éthiologie encore inconnue et dont les symptômes externes sont un œdème prononcé causant une augmentation du taux de mortalité. Une comparaison avec des tissus de truites saines indique une perte de cellularité dans les brosses glomérulaires avec remplacement des cellules mésangiales par du tissu conjonctif. Des études de l'ultrastructure démontrent que le matériel est du collagène et permettent de diagnostiquer une fibrose mésangiale glomérulaire. La lésion glomérulaire est associée à des altérations de l'épithélium qui tapisse les tubules proximaux et à beaucoup de débris à l'intérieur des lumières des tubules. Les auteurs comparent ces observations avec les lésions glomérulaires du rein des mammifères et des amphibiens.

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BECAUSE of an increase in mortality rate, a group of rainbow trout (*Salmo gairdneri*) being reared at the Pisgah Forest National Fish Hatchery, North Carolina in 1975 was examined by the regional hatchery biologist. As no evidence of an infectious disease was found, samples were sent to the Eastern Fish Disease Laboratory (EFDL) for histological examination. A tentative diagnosis of amyloidosis was made.

This unusual diagnosis was drawn to our attention. Electron microscopic examination was made and resulted in a definitive diagnosis of chronic mesangial fibrosis of renal glomeruli rather than amyloidosis. This report details the light and electron microscopic findings of the disease.

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Materials and Methods

HISTOLOGIC TECHNIQUES

Pieces of kidney (0.5 cm^3) were rapidly dissected from anesthetized fish and processed for light microscopy. Fixation was in Bouin's solution or in a mixture of 4% formaldehyde and 1% glutaraldehyde which is suitable for light and electron microscopy (McDowell and Trump 1976). Fixed tissues were dehydrated in graded ethanol solutions, cleared in xylene, embedded in paraffin, and sectioned at 5–6 μm. Sections were mounted on glass slides, deparaffinized, and stained by: hematoxylin and eosin (H&E), periodic acid-Schiff (PAS) with and without diastase controls, Van Gieson's picrofuchsin, Ver-

hoeff's elastic method, alkaline Congo red, thioflavine T, and crystal violet procedures (Lynch et al. 1969). Congo red preparations were examined under polarized light. Thioflavine T preparations were analyzed for fluorescence using a BG 12 exciter filter and an OG 4 barrier filter. All differential stains for amyloid were compared with control sections of human spleen from a patient with amyloidosis.

High-Resolution Light Microscopic Techniques

Semithin sections (0.5–1 μm) of Epon embedded tissue (see below) were stained by toluidine blue (Trump et al. 1961). Increased resolution with the thinner plastic sections permitted differentiation of endothelial, mesangial, and visceral epithelial elements of the glomerular tufts. These specimens were also used to correlate light and electron microscopic findings.

Electron Microscopic Techniques

Pieces of trout kidney (0.5 cm^3) were fixed in 4% formaldehyde and 1% glutaraldehyde in a 200 mosM phosphate buffer at pH of 7.4 (McDowell and Trump 1976). Tissues were transported and stored in the fixative until further processing. With a clean razor blade, the outside 0.5 mm of the tissue blocks were removed for electron microscopic study. Tissue blocks, 0.5 mm^3, were postfixed in 1% buffered osmium tetroxide, dehydrated in graded ethanols, and mounted in Epon (Luft 1961). Glass knives were used for semithin sections of Epon blocks and diamond knives for ultrathin sections. Ultrathin sections were stained with uranyl magnesium acetate (Frasca and Parks 1965) and lead citrate (Venable and Coggeshall 1965), mounted on carbon-coated, copper grids, and viewed with a JEOL 100B electron microscope.

Results

Gross Examination

The hatchery biologist observed fish with severe edema, pop eyes, hemorrhagic livers, and apparent anemia (pale gills). Kidneys of fresh specimens were easily removed from the dorsal body wall and spinal column.

Samples received at the EFDL had the gross external appearance of healthy hatchery trout. Internally, livers were very pale or mottled with large, red and cream-colored blotches. Apparent hemorrhages were present in the visceral fat, stomach, and pyloric ceca. The kidney was easily separated from the body wall apparently due to edema. Hematocrit values in affected fish averaged 20–25% compared with 40–50% for normal rainbow trout. In addition comparison of refractometric estimates of serum protein showed depressed values in affected fish.

Light Microscopic Findings

The histologic appearance of control (i.e. normal or unaffected) and diseased rainbow trout glomeruli is shown in Fig. 1–3. Control glomeruli did not differ from previous descriptions of freshwater teleosts including trout (Hickman and Trump 1969; Anderson and Loewen 1975). When compared to controls, virtually every glomerulus in kidneys of diseased rainbow trout revealed acidophilic regions of extracellular material in glomerular tufts (Fig. 2 and 3). Higher magnifications (Fig. 3) showed a decrease in cellularity of glomerular tufts. Hematoxylin and eosin stains of kidney showed hyaline droplets in proximal tubular epithelium.

The results of differential staining of the glomerular lesions are shown in Table 1. All tests for collagen were positive. When viewed under polarized light, the Congo red preparations showed tiny spots of green birefringence over the lesion. All other amyloid preparations were negative.

Toluidine blue stained Epon sections of glomeruli from control trout kidney (Fig. 4) showed numerous mesangial cells. Capillaries contained darkly staining red blood cells. The lamina densa of the basement membrane appeared as a thin, barely visible line which separated visceral epithelium of glomerular space from endothelial cells. Similarly stained sections

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Figures 1–3

Figures are H&E stained sections of paraffin embedded material. Fig. 1. Glomerulus (center of field) from kidney of control rainbow trout (*Salmo gairdneri*). Bowman's space (white area) surrounds glomerular capillary tufts. Nuclei of visceral epithelial, endothelial, and mesangial cells are shown. × 700. Fig. 2. Section of kidney from diseased rainbow trout at low magnification. Amorphous densely eosinophilic masses of extracellular material (arrows) are seen in glomerular tufts. × 400. Fig. 3. Higher magnification of glomerular lesion from kidney of diseased rainbow trout. Nuclei of visceral epithelial cells (arrows) are separated from capillary lumens (c) by basement membrane and by the glomerular lesion (gray area at center of field). Note hypocellularity of glomerular tuft. × 1,700.

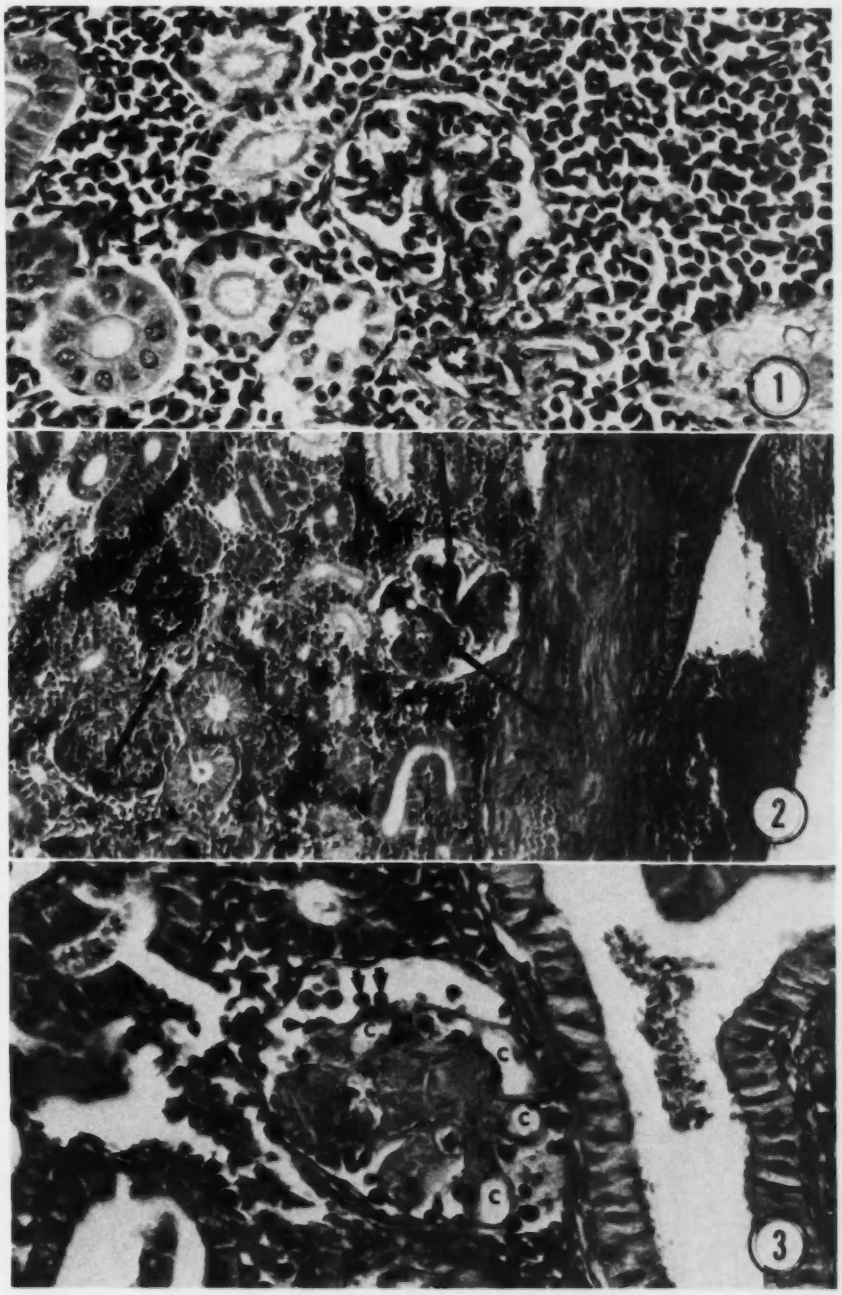
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TABLE 1. Results of differential staining on glomerular lesions

Method employed	Microscopic appearance of lesion	Interpretation[a]	Remarks
PAS with and without predigestion	Pinkish-red	mucopoly saccharide	Consistent with basement membrane thickening and/or collagen deposition.
Van Gieson's picro-fuchsin	Bright red	Collagen	Lesion revealed no khaki colored areas indicative of amyloid.
Verhoeff's elastic method	Red	Collagen	Lesion showed no evidence of elastic fiber component
Congo red	Red to pink with routine optics; tiny spots of green birefringence in polarized light	Positive for amyloid	Small component of overall lesion is amyloid
Thioflavine T (fluorescent technique)	No difference in appearance of background and lesion; both were dark blue	Negative for amyloid	Control with amyloidosis showed yellow over amyloid deposits
Crystal violet	Blue over entire lesion	Negative for amyloid	Lack of metachromasia

[a]Interpretations are based on criteria of Lynch et al. (1969).

from diseased trout kidney revealed replacement of mesangial cells by an amorphous material (Fig. 5 and 6). Isolated nuclei and cytoplasmic fragments of mesangial cells remained within the amorphous material. (Fig. 5). The lesion was clearly located within the mesangium with extensions into areas between lamina densa and endothelium (Fig. 6). Capillaries of some glomeruli appeared compressed by the deposits and contained trapped red blood cells thought to be undergoing lysis (Fig. 6). No changes were encountered in either visceral or parietal epithelium of glomeruli and afferent and efferent arterioles appeared normal.

ELECTRON MICROSCOPIC FINDINGS

The ultrastructure of control glomeruli in this study (Fig. 7) did not differ from previous accounts (Hickman and Trump 1969; Anderson and Loewen 1975). The primary ultrastructural features of the glomerular lesions are shown in Fig. 8. Between the lamina densa and endothelium and within the mesangium, large deposits of fibers were seen. These fibers revealed a cross

FIGURES 4–6

Figures are toluidine blue stains of Epon embedded material. FIG. 4. Section from kidney of control rainbow trout. Glomerulus is at center of field. Basement membrane (arrows) surrounds an area in which numerous endothelial and mesangial cells and erythrocytes (within capillaries) are found. Outside basement membrane, rounded nuclei are in visceral epithelial cells, while flattened nuclei of parietal epithelial cells surround glomerular space. × 1,700. FIG. 5. Section from kidney of diseased rainbow trout. Glomerulus is at center of field. Arrows over glomerular space point to visceral epithelial cells (podocytes). Tortuous black line is basement membrane of glomerulus. Amorphous, gray material fills mesangial region and extends between capillary endothelium and basement membrane. Arrows over amorphous material point to nuclei of mesangial cells. Note hypocellularity of mesangial space. Flattened endothelial nuclei are seen at edges of capillary (c) lumens. × 2,000. FIG. 6. Section from kidney of diseased rainbow trout. Arrows point to basement membrane. Inside basement membrane, amorphous material occupies majority of mesangial space. × 2,000.

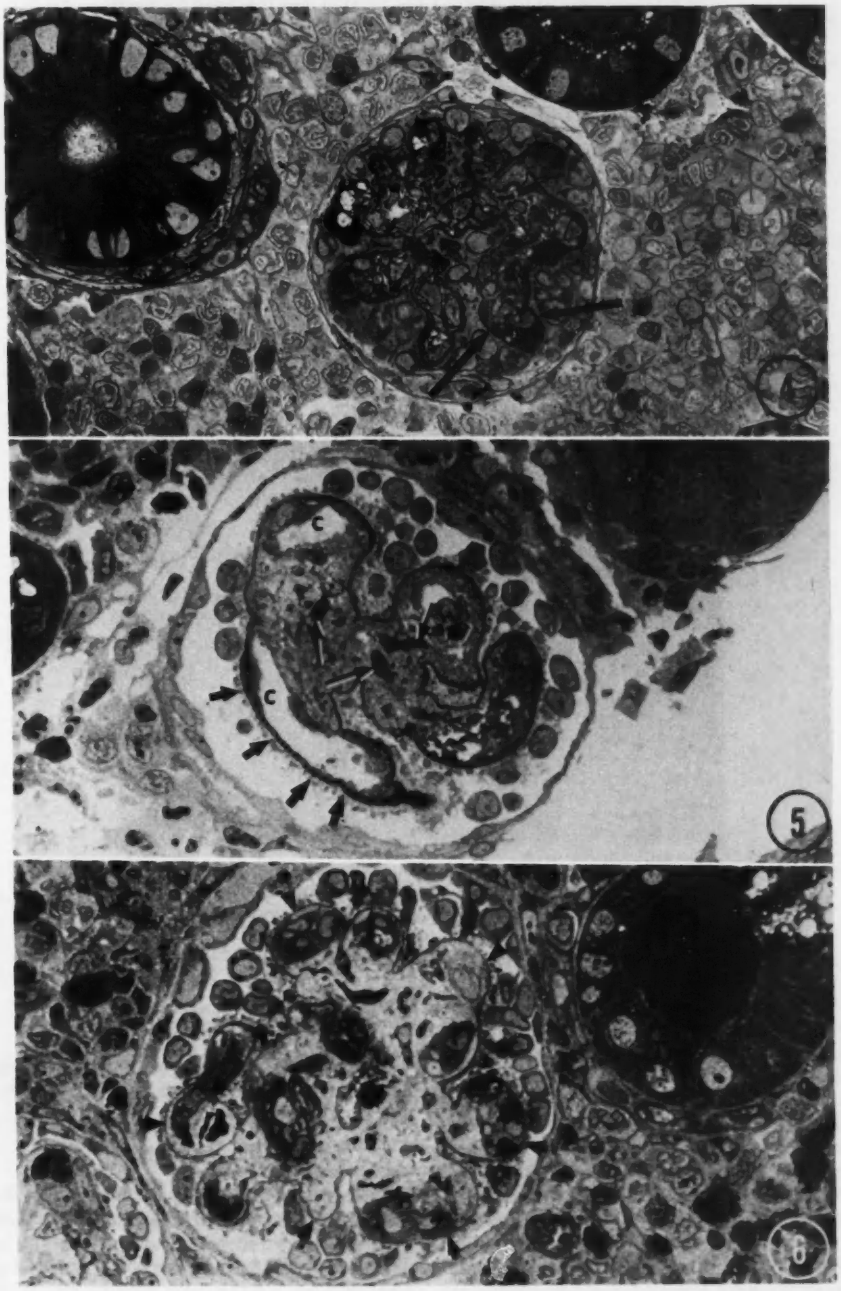
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FIG. 7. Electron micrograph of glomerulus from kidney of control rainbow trout. Basal lamina (BL) separates visceral epithelium (VE) from endothelium (En) of glomerular capillary. Dark cell at upper right-hand corner is a blood cell in capillary lumen. Uranyl magnesium acetate and lead citrate. × 10,000.

striation with a periodicity of approximately 600–640 Å indicative of collagen. Electron microscopic study of all lesions revealed no areas with the fibrillar structure of amyloid, although questionable regions between collagen fibers were observed.

Electron microscopic study of proximal tubular epithelium in diseased trout showed increased numbers of large vacuoles and phagolysosomes (Fig. 9). Extensive membranous debris was encountered in tubule lumens and similar material was seen in phagolysosomes (Fig. 9). Mitochondria with cup-shaped profiles were numerous in proximal tubular epithelium (Fig. 9).

ALTERATIONS IN OTHER ORGANS

Extreme vacuolation of exocrine pancreatic tissue was seen and further study on this lesion is now underway.

Discussion

In this report we have described alterations in renal glomeruli and proximal tubular epithelium of rainbow trout found in association with a disease of currently unknown etiology. Alterations in teleost glomerular morphology that occur as adaptations to seasonal variation and change in water salinity have been reviewed by Hickman

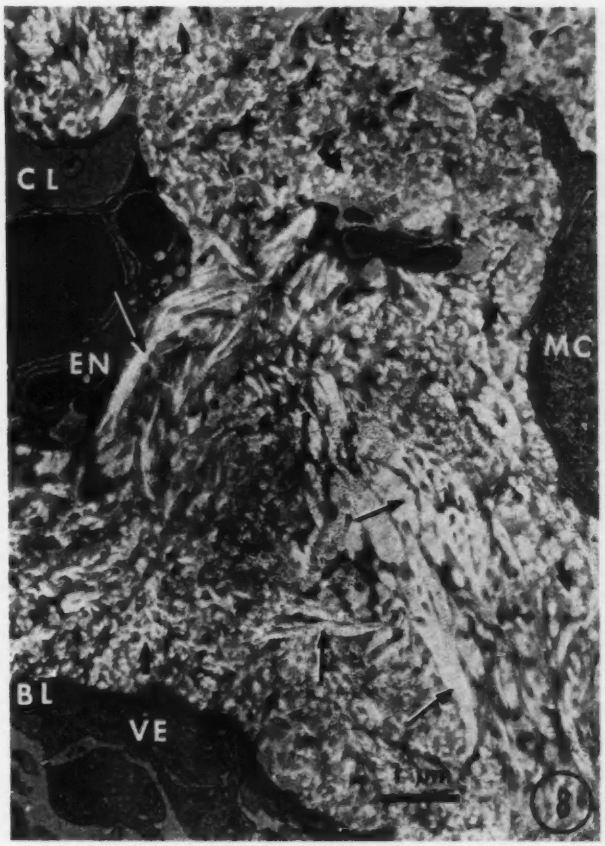

FIG. 8. Electron micrograph of glomerulus from kidney of diseased rainbow trout. Electron dense basal lamina (BL) separates visceral epithelium (VE) from large glomerular lesion. Longitudinal sections of collagen fibers in lesion reveal cross striations with regular periodicity (black and white arrows). Rounded, white profiles (small arrows) without striations are cross sections of collagen fibers. MC, mesangial cell; CL, capillary lumen; EN, endothelial cell. Uranyl magnesium acetate and lead citrate. × 12,000.

and Trump (1969). In general, the glomeruli of marine teleosts are more avascular than those of freshwater teleosts as a result of marked development of mesangial cells which produce additional basement membrane material. When the glomeruli of control trout in this study (Fig. 1 and 4) were compared to those of diseased trout (Fig. 2, 3, 5 and 6), a marked decrease in cellularity of glomerular tufts was seen with a replacement of mesangial cells by collagen fibers. Thus, the lesion shown in this study differs from the adaptive alterations in glomeruli associated with changes in salinity and seasonal variation.

Glomerular degeneration commonly accompanies kidney disease in man and other mammals (Faith and Trump 1966). Collagen fiber deposition in glomeruli occurs in a variety of disease and experimental states including: diabetic nephropathy in man (Kimmelstiel et al. 1962; Dachs et al. 1964); nail–patella syndrome, a heritable

FIG. 9. Electron micrograph of epithelium in proximal tubule from kidney of diseased trout. Membranous debris is in tubule lumen (L) near brush border (BB). Numerous apical vacuoles (AV) of varying sizes are seen. Lysosomes (ly) are numerous and some contain membranous elements. Small arrows point to cup-shaped mitochondria. N, nucleous. Uranyl magnesium acetate and lead citrate. × 10,000. For comparison with normal rainbow trout kidney see paper by Anderson and Loewen (1975).

disorder of mesenchymal tissue in man (Ben-Bassat et al. 1971); renal amyloidosis of man (Spiro 1969); experimental amyloidosis produced by casein injections or by prolonged sensitization of Arthus-type tissue antigens in the rabbit (Kimura et al. 1975); injection of rat with rabbit nephrotoxic serum (Suzuki et al. 1963); and by acute uranyl nitrate poisoning in rats (Bencosme et al. 1959). Of the above conditions, the acute uranyl nitrate poisoning in rats produced a lesion more similar to the lesion of this study as both mesangial degeneration and collagen deposition were observed. Experimental amyloidosis in the rabbit produced by injections of casein or by prolonged sensitization of Arthus-type tissue antigens resulted in extensive amyloid deposits interspaced between collagen fibrils in the basement membrane (Kimura et al. 1975). The tiny areas of green birefringence seen in Congo red preparations and the questionable areas between collagen fiber deposits in the present study could represent amyloid deposits secondary to the fibrosis. However, the major component of the lesion in the glomeruli was collagen fibers.

Focal collagen fibers, regarded by the following authors as normal, were seen in frog (Yamada 1960) and rat (Latta 1961) kidneys.

They regarded the scattered fibers, adjacent to mesangial cells, as normal in contrast to the extensive deposits seen in the present study.

We encountered alterations in proximal tubular epithelium (i.e. increased number of vacuoles containing membranous elements) coincident with membranous debris in tubule lumens. Such findings could be related to the glomerular lesions and depressed serum protein levels of the diseased trout in this study. In the nephrotic syndrome of man, alteration in glomeruli is associated with hypoproteinemia, proteinuria, and hyaline droplet formation in proximal convoluted epithelium (Golden and Maher 1971). Electron microscopically, hyaline droplets are membrane-bound protein and often appear as vacuoles containing membranes and electron-dense particles.

To date only Gossypol, a phenolic compound and the toxic element in cottonseed meal, has been shown to cause glomerular alteration in rainbow trout (Herman 1970). In that study, an increase in the PAS positive mucopolysaccharide of glomeruli was demonstrated.

Fish from the same source as those of this study reared in geographically different sites but fed a diet from the identical supplier, have not been shown to have overt signs of disease. The possibility is therefore raised that a waterborne toxin, in synergism with dietary factors, could be the etiologic agent in glomerular mesangial fibrosis of rainbow trout. Since the water in which the affected fish were reared is from a well-protected source (a stream from forest land where pesticides are not used) and is low in mineral content, the likelihood of a pesticidal or industrial heavy metal etiologic agent is small.

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Deteriorative Changes During Frozen Storage in Fillets and Minced Flesh of Silver Hake (*Merluccius bilinearis*) Processed from Round Fish Held in Ice and Refrigerated Sea Water

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HILTZ, D. F., B. S. LALL, D. W. LEMON, AND W. J. DYER. 1976. Deteriorative changes during frozen storage in fillets and minced flesh of silver hake (*Merluccius bilinearis*) processed from round fish held in ice and refrigerated sea water. J. Fish. Res. Board Can. 33: 2560–2567.

During frozen storage at −10 C, deterioration in muscle of silver hake (*Merluccius bilinearis*) was marked by rapid and extensive production of dimethylamine, concomitant decrease in extractable protein, and by lipid hydrolysis. Evidence of lipid oxidation in this gadoid species of relatively high fat content (2–4%) was also obtained. In minced flesh the rates of deterioration were about twice as fast as in fillets. Holding round fish for up to 6 days in refrigerated sea water (RSW) at 0–1 C before processing extended the frozen storage life of fillets at −10 C by 2–3 wk and of minced flesh by 1 wk over that for comparable materials prepared from round fish held in ice. Materials prepared from winter (March) and summer (August) fish showed little or no difference in rates of deterioration. The susceptibility of silver hake to deterioration at −10 C is similar to cusk; deterioration is faster than in cod or haddock, but not as fast as in red hake (*Urophycis chuss*). In all silver hake materials negligible deterioration occurred during frozen storage at −26 C for up to 6 mo.

During preprocessing storage of round silver hake in RSW, a firm texture and acceptable appearance were retained for several days longer than in round fish held in ice, where objectionable softening of the flesh occurred, particularly in summer-caught fish. Saturation of the sea water with CO_2 retarded the onset of bacterial spoilage in RSW-held fish, which otherwise developed more rapidly than in iced fish.

HILTZ, D. F., B. S. LALL, D. W. LEMON, AND W. J. DYER. 1976. Deteriorative changes during frozen storage in fillets and minced flesh of silver hake (*Merluccius bilinearis*) processed from round fish held in ice and refrigerated sea water. J. Fish. Res. Board Can. 33: 2560–2567.

Au cours de l'entreposage réfrigéré à −10 C, la détérioration dans le muscle du merlu argenté (*Merluccius bilinearis*) se manifeste par une production rapide et abondante de diméthylamine, par une diminution concommittante des protéines extractibles et par l'hydrolyse des lipides. On constate également une oxydation des lipides chez ce gadidé à teneur en gras relativement élevée (2–4%). La vitesse de détérioration est à peu près 2 fois plus grande dans la chair hachée que dans les filets. Le fait de maintenir des poissons entiers pour une période allant jusqu'à 6 jours dans de l'eau de mer réfrigérée (EMR) à 0–1 C avant la transformation prolonge la durée d'entreposage réfrigéré des filets à −10 C de 2–3 semaines, et celle de la chair hachée de 1 semaine de plus que celle de matériel comparable préparé à partir de poissons entiers maintenus dans la glace. Le matériel préparé à partir de poissons d'hiver (mars) et d'été (août) ne manifeste que peu ou pas de différence dans la vitesse de détérioration. La susceptibilité du merlu argenté à la détérioration à −10 C est semblable à celle du brosme; la détérioration est plus rapide que chez la morue ou l'aiglefin, mais pas aussi rapide que chez la merluche-écureuil (*Urophycis chuss*). Dans tout le matériel provenant du merlu argenté, il ne se produit q'une détérioration négligeable durant l'entreposage réfrigéré à −26 C sur une période allant jusqu'à 6 mois.

Durant l'entreposage de prétransformation de merlu argenté rond dans de l'EMR, le poisson conserve une texture ferme et une apparence acceptable sur une période plus longue de plusieurs jours que le poisson rond maintenu dans la glace, où il se produit un amollissement indésirable des chairs, surtout chez des poissons capturés en été. La saturation de l'eau de mer avec du CO_2 retarde le début de la décomposition bactérienne dans du poisson maintenu dans l'EMR, qui, sans cela, se développe plus rapidement que chez les poissons maintenus dans la glace.

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SILVER hake (*Merluccius bilinearis*) are exploited extensively on the continental shelf of eastern North America by the USSR, and to a lesser extent by the U.S. (Jones 1974), but are not currently utilized by Canadian fishermen. Recently, however, the Canadian fishing industry has been directing increased attention to the potential of underexploited species, because of declining stocks of traditional groundfish and the growing diversification into secondary fishery products, especially those utilizing minced flesh (Anon. 1974). This situation prompted a collaborative study on silver hake by the Resource Development Branch, Nova Scotia Department of Fisheries, whose interests lay in the delineation of effective areas and periods of the fishery within our waters, and the Halifax Laboratory, who were concerned mainly with the factors affecting stability of this species in frozen storage. The present paper reports our findings in the latter investigation.

The hake species, in general, have a poor reputation for keeping quality in fresh and frozen storage. The flesh is characteristically soft, a condition that worsens with time of chill storage. Silver hake are relatively small fish, averaging 30 cm long (Jones 1974), and in the New England area are commonly landed ungutted, frequently without ice (Mendelsohn and Peters 1963). Gloucester technologists have demonstrated the potential importance of refrigerated sea water (RSW) at −1 C vs. ice for extending the chilled storage life of round hake and the subsequent frozen storage life of dressed fish (Cohen and Peters 1963a, b; Peters et al. 1963), and have recently developed new products of good commercial potential as alternatives to the traditional frozen packs of headed, dressed silver hake (Anderson and Mendelsohn 1971).

We had established previously (Lall et al. 1975) that silver hake, in common with other gadoids (Castell et al. 1971), has the capability to form dimethylamine (DMA) and formaldehyde in the flesh by enzymatic degradation of trimethylamine oxide. The present study confirms this finding and includes definition of the rate and extent of DMA formation and of the accompanying deteriorative changes in protein and lipid constituents in the muscle of silver hake during frozen storage; in attempts to improve storage quality, the effects of some variations in prefreezing condition and treatment were also studied.

Materials and Methods

FISH

The winter fish were caught early in March 1974 in Emerald Basin at a depth of 170–190 m by a commercial trawler under charter to the province of Nova Scotia. Most of the fish were small, 23–30 cm long. On decking, one lot of several hundred kilograms was well iced, round, in boxes. Another similar lot of round fish was distributed between two RSW tanks to give a density of about 2 kg fish/liter of sea water (20 lb/gal). Although the optimum temperature for RSW is −1 C, the tanks were maintained at 0–1 C to minimize freezing up of equipment on the vessel. A third, smaller lot of somewhat larger fish (up to 45 cm long) was gutted and washed, then well iced. Upon landing at Halifax, some round fish of each lot in ice and RSW were processed at once (2 days from catching); the remainder were held in the original containers of ice and RSW for 4 and 6 days from the time of catching before processing. To determine the effect of prolonged holding of round fish under these two conditions, the fish were also examined for quality after 9 and 11 days in ice and RSW, but none were processed for frozen storage at these times. The fish gutted at sea were held 4 days in ice before processing.

The summer fish were trawled as above in mid-August 1974 on Sable Island Bank and had been well iced, round, on the vessel for 24 h when landed. These fish were similar in size to winter fish, and most were in a spawning or pre-spawning condition. At the laboratory, one lot of round fish was held well iced in insulated boxes, a second placed in a tank of RSW as above, and a third maintained in another tank of RSW kept saturated with carbon dioxide (gas) to minimize bacterial activity during the holding. By this treatment, the pH of RSW was lowered to 5.7–5.9 during the storage period compared with 6.7–6.9 for untreated RSW. The fish were held in ice, RSW, and RSW–CO_2 for 2 and 5 days from the time of catching before processing.

PROCESSING

At 2, 4, and 6 days in ice and RSW (winter fish), and at 2 and 5 days (summer fish), the fish were headed, gutted, and washed (H&G) under commercial conditions, and processed in various ways to obtain intact and minced flesh for frozen storage studies. Mincing was accomplished by passing the material through a Bibun meat-separator (Models DX-15 or SDX-16) fitted with a drum having 5-mm holes. The winter fish were processed as intact, skinless fillets and as three kinds of minced material prepared from skinless fillets, H&G fish, and H&G fish from which about two thirds of the backbone had been removed to minimize blood and traces of kidney tissue in the mince (Dingle and Hines 1975). The winter fish, gutted at sea and held 4 days in ice, were processed as minced flesh from skinless fillets and H&G fish only. All materials were packaged in about 100-g lots in small polyethylene bags, packed in groups of 3 bags per 0.5 kg wax-coated cardboard carton, and quick-frozen in a plate freezer at −40 C. The cartons were placed in large polyethylene bags for storage in constant-temperature cabinets at −10 ± 0.2 C (+14 F); this temperature is high enough to permit reasonably rapid development of DMA and other deteriorative changes in the muscle,

TABLE 1. Quality changes in silver hake (*Merluccius bilinearis*) during holding as round fish in ice and RSW (sl. = slightly; v. = very; ext. = extremely).

Age from catching (days)	Appearance of flesh	Inspection grade[a]	Taste panel rating[b]		TMA (*mg N/100 g*)	NaCl (*% wet wt*)
			texture	flavor		
		Winter fish				
Ice						
2	firm	I	78	86	0.2	0.32
4	softening; no odor	I	77	76	0.5	0.30
6	quite soft; no odor	I-II	69	73	0.5	0.32
9	v. soft; sl odor	III	55	69	2.1	0.18
11	ext. soft; off-odors	III	46	52	3.8	—
RSW						
2	firm	I	84	90	0.1	0.57
4	firm	I	81	81	0.6	0.88
6	firm; off-odors	I-II	77	77	10.4	0.85
9	softening; putrid	III	—	—	22.6	1.09
		Summer fish				
Ice						
2	sl. soft	I	79	83	0.2	0.16
3	sl. soft; no odors	I	—	—	0.5	—
4	soft; gut odors	II	73	66	0.6	—
5	v. soft; gut odor on flesh	II-III	66	69	2.4	0.14
RSW						
2	firm	I	83	86	0.3	0.37
3	firm; no odors	I	—	—	0.5	—
4	firm; sl. off-odors	II	76	76	1.2	—
5	firm; off-odors	III	78	73	2.5	0.82
RSW-CO_2						
2	firm	I	83	81	0.3	0.44
3	firm	I	—	—	—	—
4	firm	II	67	63	0.5	—
5	softening; no odors	II	73	56	0.7	0.85

[a]Grades: I = top quality, free of perceptible spoilage; II = incipient spoilage; III = reject quality (definitely spoiling or unacceptable appearance).

[b]Values given are the averages of 10–16 judgements per sample; with the numerical scoring system used (Dyer et al. 1964b) ranging from 100 (perfect) to 0 (very badly spoiled), 40 represents the limit of acceptability.

and moreover, may frequently be reached in commercial practice, especially within the distribution and marketing chain (e.g. Peters 1964). Controls of each lot were stored at −26 C (−15 F).

Examination and Analysis

During preprocessing holding in ice and RSW, the round fish were examined for changes in organoleptic properties and were assigned grades by two experienced field officers of Inspection Branch, Fisheries and Marine Service, according to the Service's specifications. Changes in eating quality were followed by taste panel evaluation of baked samples for texture and flavor, according to established procedures (Dyer et al. 1964b). The onset of bacterial spoilage was monitored by measurement of trimethylamine nitrogen (TMA-N) (Dyer 1959) on composite samples of flesh from six to eight fish. Similar composite samples were used for sodium determination by flame emission spectrophotometry (AOAC 1970) after ashing and treatment of ash with concentrated nitric acid. Results were expressed as percent NaCl in the flesh.

During frozen storage of the various materials at −10 and −26 C, deteriorative changes were followed by monitoring the rates of accumulation of dimethylamine nitrogen (DMA-N) (Dyer and Mounsey 1945) and of the accompanying decrease in extractable protein nitrogen (EPN) (Dyer et al. 1964a). Lipid hydrolysis and oxidation were followed by determination of the contents of free fatty acid (FFA) (Bligh and Scott 1966) and of malonaldehyde by the thiobarbituric acid reaction (TBA) (Vyncke 1970), respectively. Total lipids were extracted according to Bligh and Dyer (1959).

Results

Quality Changes in Round Fish During Preprocessing Storage in Ice and RSW

The progression of changes in organoleptic and related properties for both winter and summer silver hake is summarized in Table 1. A predominant change early in the storage period was the softening of the flesh of fish held in ice: with

winter-caught hake, this condition was first evident at 4 days and worsened rapidly, making handling and processing difficult. The summer fish held in ice softened even more quickly and were considered unmarketable by fishery inspectors at about 5 days. In contrast, holding in RSW at the same temperature maintained the firm texture of the flesh and excellent appearance of summer and winter fish for 5–6 days, due probably to the substantially reduced pressure on the soft flesh of silver hake in this medium compared with ice. Unfortunately, fish held in RSW without CO_2 suffered premature quality loss because of rapid bacterial buildup indicated by strong spoilage odors in the tank water; spoilage of the flesh was confirmed by elevated TMA-N levels, particularly in the winter fish at 6 days. (We suggest that a lower seawater temperature (e.g. −1 C) than that used (0–1 C) may be necessary to alleviate this difficulty.) The use of CO_2 to exclude oxygen and lower the pH substantially reduced the problem, although some softening of the flesh was apparent at 5 days compared with the firm texture of fish held in RSW without CO_2.

Taste panelists rated baked silver hake fillets prepared from both winter and summer fish highly acceptable initially (2 days from catching). The flavor was bland, characteristic of gadoid species; the texture, flaky and tender, was described as similar to that of sole. Good-to-fair eating quality was maintained to 6 and 5 days for the winter and summer fish, respectively, in ice and RSW. Texture scores for the iced fish at these times were slightly lower than those for the RSW-held fish because of increasing mushiness, a reflection of the softness of the raw flesh. In the cooked fillets prepared from RSW fish, slight saltiness was noted by some tasters at 4 days, and slight-to-moderate saltiness at 5–6 days, concomitant with increased salt uptake in the raw flesh. These salt concentrations (0.82–0.85%) were not objectionable, but rather enhanced acceptability of this bland species.

These results indicate that silver hake should be processed as soon as possible after capture (preferably within 2–3 days) to ensure a quality product at the retail level. Similar recommendations (no more than 5 days on ice) have been advanced by Mendelsohn and Peters (1963) and Varga et al. (1974).

Frozen Storage Changes in Fillets and Minced Flesh from Round Fish Held in Ice and RSW

In all control samples stored at −26 C, there was negligible change from the initial values in any of the properties tested up to 25 wk storage. At −10 C, on the other hand, rapid and extensive deterioration occurred, as measured by changes in concentrations of DMA, EPN, and FFA.

Dimethylamine — In materials prepared from winter-caught silver hake held in ice before processing (Fig. 1), rates of DMA formation were considerably faster than in those prepared from fish held in RSW. Time of holding in ice (up to 6 days) had little or no effect; prolonged holding in RSW, however, slowed subsequent rates of DMA formation on frozen storage appreciably. In this case, elevated TMA concentrations in the RSW-held fish at 6 days (Table 1) may have had an inhibitory effect on the activity of the DMA-producing enzyme (Tomioka et al. 1974); slow DMA production was also observed in Alaska pollock muscle (Tokunaga 1964) spoiled at the time of freezing. There may also have been a leaching effect with consequent loss of reactants (TMAO) or cofactor(s) for the enzymic system during holding in RSW.

Minced flesh of silver hake prepared from H&G and from backbone removed fish (C and D) tended to form DMA faster than intact fillets or minced fillets (A and B), regardless of preprocessing holding medium. In the minced materials prepared from the one lot of fish gutted at sea and held 4 days in ice, rates of DMA formation did not differ significantly from those in corre-

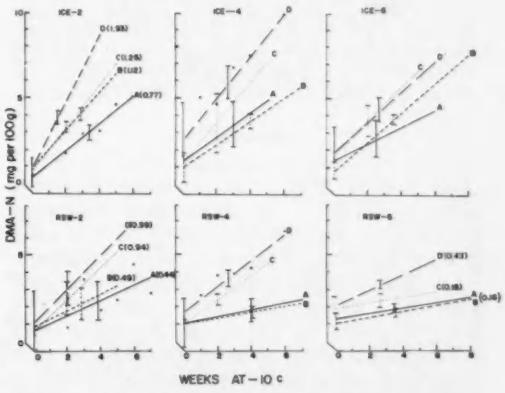

FIG. 1. Dimethylamine accumulation during frozen storage at −10 C in fillets and minced flesh of winter-caught silver hake (*Merluccius bilinearis*) held 2, 4, and 6 days as round fish in ice and RSW before processing. A, Skinless fillets; B, minced fillets; C, minced flesh prepared from backbone-removed, headed and gutted fish; and D, minced flesh prepared from headed and gutted fish. Slopes of some of the regression lines are given in parentheses. Points for some lines are plotted to illustrate degree of scatter. 95% confidence limits of the mean at $x = 0$ and at $\bar{x}$ are shown. All regression lines were significant at the 5% level; numbers of samples ranged from 5 to 8.

sponding materials prepared from 4-day iced round fish.

In summer-caught silver hake (Fig. 2), rates of DMA formation in intact and minced flesh were similar to those in corresponding materials of the winter fish. Holding conditions before processing also showed many of the same trends: in general, rates were faster after storage of round fish in ice than in RSW and significantly faster in minced flesh than in fillets; slower rates were observed after RSW storage for 5 days than for 2 days. Preprocessing holding in RSW–CO_2 compared with RSW alone appeared to slow subsequent rates of DMA formation in minced materials but not in fillets.

Extractable protein nitrogen — Loss of protein solubility occurred concomitantly with DMA formation in all materials prepared from the winter- and summer-caught silver hake (Fig. 3 and 4). Rates of EPN decrease (winter fish, Fig. 3) were usually faster following preprocessing holding in ice than in RSW and were considerably accelerated in minces (C & D) compared with intact flesh (A). Rates in summer fish (Fig. 4) were similar to those in like materials of winter fish. As with DMA production, loss of EPN, particularly in minced materials from winter fish, was slower with longer time of preprocessing holding in RSW. Inexplicably, however, the initial (zero-time) EPN values in the minces were significantly lower (5% level) after 4–6 days holding in RSW than at 2 days; this, as well as rate of EPN decrease, will be a determining factor in estimations of frozen storage life from EPN data (see below).

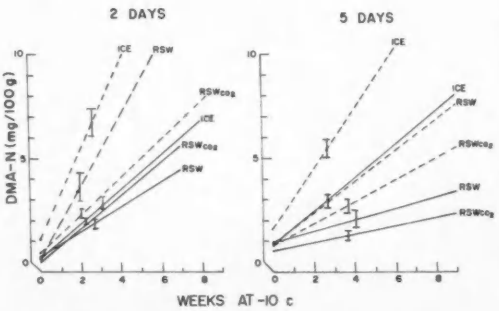

FIG. 2. Dimethylamine accumulation during frozen storage at −10 C in fillets and minced flesh of summer-caught silver hake held 2 and 5 days as round fish in ice, RSW, and RSW–CO_2 before processing. Solid lines, skinless fillets; dotted lines, minced flesh prepared from headed, gutted fish. 95% confidence limits of the mean at $\bar{x}$ are shown. The regression lines were significant at the 5% level; numbers of samples ranged from 9 to 13.

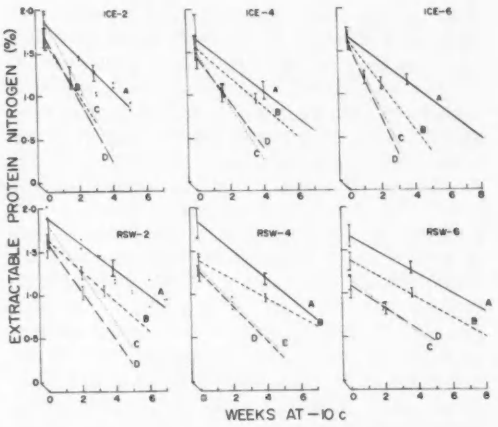

FIG. 3. Decrease in extractable protein nitrogen during frozen storage at −10 C in fillets and minced flesh of winter-caught silver hake. Materials and preprocessing conditions as in Fig. 1. 95% confidence limits of the mean at $x = 0$ and at $\bar{x}$ are shown. All regression lines were significant at the 1% level; numbers of samples ranged from 8 to 16.

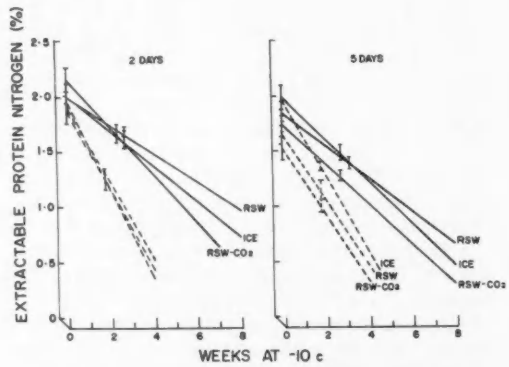

FIG. 4. Decrease in extractable protein nitrogen during frozen storage at −10 C in fillets and minced flesh of summer-caught silver hake. Materials and preprocessing conditions as in Fig. 2. 95% confidence limits of the mean at $x = 0$ and at $\bar{x}$ are shown. All regression lines were significant at the 1% level; numbers of samples ranged from 16 to 20.

Lipid hydrolysis and oxidation — Silver hake have more fat than other gadoid species; the total lipid content of the flesh of winter fish (all materials) averaged 1.90% (±0.05 SE for 87 samples), compared with <1% in the flesh of cod, haddock, Atlantic pollock, and cusk. The range of lipid concentrations observed, 0.90–3.4%, probably reflects varying amounts of red muscle in the samples of silver hake analyzed.

The silver hake has a wide lateral band of "red" (creamy brown) muscle just under the skin, extending the length of the fish and becoming thicker (up to 2 mm) near the tail. The lipid concentrations of three samples of red muscle, each a composite from six fish, were 12.3, 11.9, and 19.5%, compared with 0.92, 0.86, and 0.96% in composite samples of ordinary muscle from the same fish.

Variation in lipid content among materials prepared from summer-caught silver hake is as follows (CL = confidence limits):

	n	Avg % lipid	SE	95% CL
ICE				
Fillets	24	2.95	0.12	2.70–3.20
Minces	26	2.20	0.06	2.07–2.32
RSW				
Fillets	52	3.67	0.12	3.44–3.91
Minces	51	2.37	0.04	2.30–2.45

The lipid content in the flesh of the summer (spawning) fish was higher than that of the winter fish. In addition, unlike the winter fish, significant differences in lipid content (5% level) were found between intact and minced flesh and between materials prepared from fish held in ice and RSW. The lower lipid concentration in minced flesh than in fillets may be due to the removal of more fatty subcutaneous tissue and red muscle with skin by the mechanical deboning process than by hand-skinning of the fillets. Similarly, more red muscle may have been removed by hand-skinning of fillets from the soft iced fish than from the firmer-fleshed, more easily handled RSW fish, thus accounting for lower lipid levels in the fillets from iced fish. The differences were not due to moisture content, which was similar in fillets from iced and RSW fish (80.7%). Although the minced flesh had a significantly higher moisture content (82.3%) than fillets, this difference was insufficient to account for the lower lipid content of the minced material.

Extensive lipid hydrolysis (accumulation of FFA) occurred in all samples of winter and summer silver hake during 2-mo storage at −10 C (Fig. 5). The rate and extent of FFA increase was the same for all materials regardless of preprocessing storage condition or of processing technique (fillets or minced flesh). However, materials prepared from summer fish held in RSW for 5 days had significantly lower levels of FFA initially and throughout the storage period.

Oxidative rancidity as measured by the TBA reaction developed to some degree in all samples; maximum values of 3–5 μmole malonaldehyde/100 g were recorded in some minced materials after 4–7 wk at −10 C. However, extreme fluctuations in the levels were observed and may have been caused by varying amounts of lipid-rich red muscle in the samples analyzed. A few taste tests conducted on the fillet samples after 8–9 wk at −10 C (close to the limit of acceptability) indicated the presence of slightly rancid off-flavors, although textural toughening was the main factor in reduced acceptability at this time.

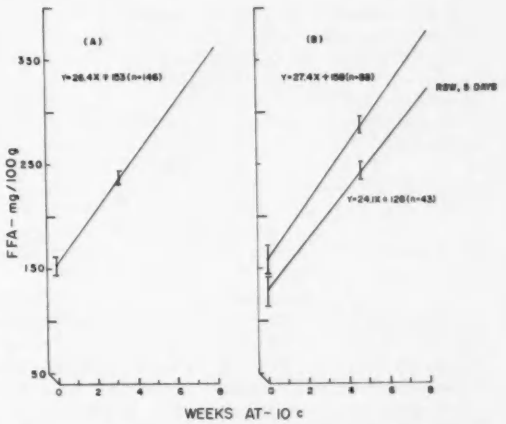

FIG. 5. Accumulation of free fatty acid during frozen storage at −10 C in muscle of silver hake. A, Winter-caught fish, all materials (see legend of Fig. 1); B, summer-caught fish, materials prepared from fish held round in RSW and in RSW–CO_2 for 5 days before processing (lower line); all other materials (see legend of Fig. 2) (upper line).

Discussion

The rapid and extensive deterioration observed during frozen storage at −10 C appears to be associated chiefly with the capability of silver hake to form DMA-formaldehyde, with the accompanying protein insolubilization that leads to textural toughening (Dyer 1973; Castell et al. 1973; Tokunaga 1974). Decrease in EPN correlates well with production of DMA (Fig. 6) during frozen storage of the silver hake materials at −10 C. A similar relationship has been noted for other gadoids (Castell et al. 1973; Dingle and Hines 1975). Considerable loss of protein extractability occurred at relatively low levels of DMA, e.g. about 50% inextractable at DMA of 3 mg N/100 g; indeed, at the point of complete inextractability of the myofibrillar protein fraction (~EPN of 0.6%), DMA levels did not exceed 6 mg N/100 g. For materials prepared from summer fish held in ice, however, it was apparent that more DMA–formaldehyde was required to effect a given EPN decrease (DMA > 7

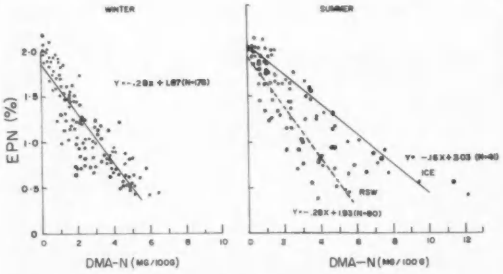

FIG. 6. Relation between DMA formation and EPN loss in muscle of silver hake during frozen storage at −10 C. For the winter-caught fish, data for all materials (see legend of Fig. 1) have been used; for summer-caught fish, separate regression lines are plotted for materials prepared from fish held under each of the two preprocessing holding conditions: ice and RSW with and without CO_2.

mg N/100 g at EPN 0.6%), suggesting that the DMA-producing ability of silver hake muscle may vary with season or possibly with catching area as indicated for Alaska pollock muscle by Tokunaga (1974).

There is strong evidence (Castell et al. 1973) that the degradative mechanism involving formaldehyde is favored over protein aggregation involving the formation of complexes between proteins and fatty acids or their oxidation products, even though appreciable FFA accumulation also occurs in silver hake. The "fattier" silver hake is relatively high in neutral lipid compared with other gadoids (about 70% of the total lipid in six samples of muscle examined; J. C. Sipos and R. G. Ackman personal communication); however, the possible protective effect that neutral lipid may have on protein denaturation, as postulated for fish species of similar lipid content like ocean perch and sole (Hanson and Olley 1965), is obviously overridden in the case of silver hake by the presence of highly active formaldehyde.

We estimated the average maximum storage life (in weeks) at −10 C for the various materials prepared from winter- and summer-caught silver hake, assuming that the texture will have become unacceptably tough at or near an EPN of 0.6% (Dyer 1951), to be:

	Winter fish		Summer fish		
	Ice	RSW	Ice	RSW	RSW–CO_2
Intact fillets	7	9	8	10	7
Minced fillets	4	7	—	—	—
Minced backbone removed	3	4	—	—	—
Minced, H&G	3	4	3	4	4

The keeping times for materials prepared from summer fish were similar to those for corresponding materials from winter fish, despite the softer flesh of the summer fish at the time of freezing. For fish caught at both seasons, holding in RSW (without CO_2) at 0–1 C before processing clearly extended the frozen storage life over that for fish held in ice at the same temperature; the extended shelf life was 2–3 wk for intact and minced fillets and 1 wk for other minces. In the ice-held fish, there may have been some cellular damage to the characteristically fragile flesh of silver hake by pressure of the ice and by the handling during icing. Peters et al. (1963) showed that the storage life of dressed hake at −18 C was 2–4 mo longer for fish held in RSW (−1 C) before processing than for fish held in ice. In the present work, the minced silver hake materials deteriorated about twice as fast as intact flesh, although minced fillets from RSW fish had greater stability. A more rapid deterioration in minced flesh compared with fillets was also found for Pacific hake, *M. productus* (Babbitt et al. 1972) and for cod and Atlantic pollock in the presence of gadoid kidney tissue (Dingle and Hines 1975). Significant amounts of kidney tissue are not likely to be present in minces prepared from silver hake because of the kidney's anterior location in this species, almost within the head, enabling effective removal during beheading. The instability of silver hake minces was probably enhanced by the presence of considerable amounts of red muscle, known to be an active source of the enzyme catalyzing DMA-formaldehyde formation (Castell et al. 1971; Tokunaga 1974), although blood, particularly in minces from H&G fish, may also be involved (Dingle and Hines 1975).

The estimated maximum storage life at −10 C of fillets of silver hake cut from iced fish (7 wk) is comparable to that in fillets of cusk and Atlantic pollock at this temperature (7 wk, W. J. Dyer et al. unpublished data); it is considerably shorter than that of cod (>10 wk), but not as short as that of red hake, *Urophycis chuss* (5 wk) (Dyer and Hiltz 1974). The fact that negligible deterioration occurred in silver hake materials at −26 C for up to 6 mo emphasizes the importance of low temperature storage and avoidance of temperature "shock" during distribution and marketing (Dyer and Hiltz 1974) for maintaining the quality of this species in frozen storage. Moreover, inactivation of the formaldehyde-producing enzyme by heat treatment, as used by Lall et al. (1975), before (or during) processing would markedly improve frozen storage stability of secondary products utilizing intact or minced flesh of silver hake.

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Respiration Rates, Energy Budgets, and Molting Frequencies of Three Species of Euphausiids Found in the Gulf of St. Lawrence[1]

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SAMEOTO, D. D. 1976. Respiration rates, energy budgets, and molting frequencies of three species of euphausiids found in the Gulf of St. Lawrence. J. Fish. Res. Board Can. 33: 2568–2576.

Respiration rate experiments at different temperatures were conducted on three species of euphausiids, *Meganyctiphanes norvegica*, *Thysanöessa raschii*, and *T. inermis*, found in the Gulf of St. Lawrence. The slopes of the respiration regression lines at different temperatures for the same species were not significantly different. *Thysanöessa inermis* acclimated to temperature changes with the result that its respiration rates remained relatively stable over most of the temperatures tested.

Feeding rates were measured for *M. norvegica* and *T. inermis* at different temperatures using *Artemia* nauplii as food. The number of calories ingested, expressed as a percentage of the total body calories of the euphausiid, decreased with body size and water temperature. *Thysanöessa inermis* ingested fewer calories than *M. norvegica* in relation to total body calories at all temperatures. Both species showed a linear relationship between molting frequency and water temperature, *T. inermis* having a shorter intermolt period than *M. norvegica*.

Results were used to estimate the energy consumption of the natural populations of euphausiids in the upper part of the Gulf of St. Lawrence estuary.

SAMEOTO, D. D. 1976. Respiration rates, energy budgets, and molting frequencies of three species of euphausiids found in the Gulf of St. Lawrence. J. Fish. Res. Board Can. 33: 2568–2576.

Nous avons déterminé expérimentalement les taux de respiration à différentes températures chez trois espèces d'euphausides, *Meganyctiphanes norvegica*, *Thysanöessa raschii* et *T. inermis*, trouvées dans le golfe Saint-Laurent. La pente des droites de régression de la respiration à différentes températures ne diffère pas de façon significative pour une même espèce. *Thysanöessa inermis* s'acclimate aux changements de température et, comme résultat, son taux de respiration demeure relativement constant à la plupart des températures d'essai.

Nous avons mesuré les taux d'alimentation de *M. norvegica* et de *T. inermis* à différentes températures, utilisant des nauplii d'*Artemia* comme nourriture. Le nombre de calories absorbées, exprimé en pourcentage des calories du corps entier de l'euphauside, diminue en fonction de la taille et de la température de l'eau. *Thysanöessa inermis* absorbe moins de calories que *M. norvegica* par rapport au nombre de calories du corps entier à toutes les températures. Chez les deux espèces, la fréquence de mue est en fonction linéaire de la température de l'eau, la période d'intermue étant plus courte chez *T. inermis* que chez *M. norvegica*.

Ces résultats ont été utilisés pour estimer la consommation d'énergie des populations naturelles d'euphausides dans la partie supérieure de l'estuaire du golfe Saint-Laurent.

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THREE species of euphausiids, *Meganyctiphanes norvegica*, *Thysanöessa raschii*, and *T. inermis*, are common in the Gulf of St. Lawrence near the Gaspé coast. Studies by Sameoto (1972) and Berkes (1973) showed that large concentrations of the three species existed during May and June with lesser concentrations occurring in September and December. The water temperature along this coast below 25 m depth ranges from 0 to 4 C for the entire year with the water above 25 m depth reaching 15 C during the summer months. The euphausiids undergo a vertical migration every 24 h that takes them through a temperature range of 15 C (Sameoto 1976). Little attention has been paid to the problems of respiration rates and energy consumption of these species in cold waters, and most studies have been concerned with populations found in water above 5 C.

[1]Bedford Institute of Oceanography Contribution.

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This study was conducted to obtain data on the molting frequency, respiration rates, and feeding rates of the three euphausiid species in the Gulf with the aim of using the data to calculate the energy requirements of natural populations near the Gaspé coast.

Materials and Methods

Respiration Rate Experiments

All the euphausiids used in experiments were collected in the Gulf of St. Lawrence and were fed 48-h-old *Artemia* larvae while being acclimated to the experimental temperatures for 10 days. They were then placed in 125- or 300-ml glass stoppered bottles, depending on the size of the animal, containing filtered sea water at the experimental temperature. The bottles were kept in the dark for 24 h in a water bath with an accuracy of ± 0.25 C. At the end of the experiment 60 ml of water was siphoned out of the experimental bottle and the oxygen content determined by the Winkler method using 0.005 N thiosulfate. The animal was removed, rinsed in distilled water, dried at 70 C for 48 h, and then weighed.

The shipboard experiments were conducted on animals collected minutes before experiments were run at ambient water temperature. The procedure for determining O_2 content was the same as above.

Feeding Experiments

Known numbers of live 48-h-old *Artemia* nauplii were added to beakers containing one euphausiid in 1000 ml of filtered (Whatman GF/A glass fiber) sea water. The euphausiid was transferred to new sea water containing new nauplii every 24 h. The nauplii remaining in the water after 24 h of feeding were killed with Formalin and counted. Partially eaten nauplii were also counted.

A Sony videocorder and television camera connected to a projecting microscope were used to record the number of live nauplii being added to the beaker. The video tape was played back and stopped to freeze the movements of the nauplii on the television monitor to get an accurate count of the number of nauplii being added to the beaker. The error in this method was ±1%. At the end of the feeding experiment the euphausiids were rinsed in distilled water, dried at 70 C for 72 h, and weighed.

Molting-Frequency Experiments

The animals used in the molting-frequency experiments were kept in beakers containing 1000 ml of sea water. A greater number of nauplii than the euphausiids could eat were added each day when the water was changed and checked for molts. The animals were kept in the dark at all times other than when the water was changed. The molts were rinsed in distilled water, dried at 70 C, and weighed. The carapace length was measured each time the animal molted to detect any growth. After the euphausiid molted several times it was killed and weighed after drying at 70 C for 72 h. Animals in the feeding and molting experiments were kept in a water bath with an accuracy of ±0.25 C.

The dry weights of 48-h-old nauplii were determined by placing a known number of nauplii rinsed with distilled water on preweighed drying pans and drying at 70 C for 48 h. Weights were determined using a Cahn Electrobalance. The caloric values of nauplii were measured using a Phillipson microbomb calorimeter. Attempts were made to feed the euphausiids exclusively on single species cultures of the phytoplankters *Flagellaria* and *Monochrysis* and a mixed species group of copepods (the largest being *Calanus finmarchicus*) but these failed. Since it was important to know the amount of energy the euphausiids were ingesting, it was decided, on the basis of ease of handling and measurement, to use only *Artemia* nauplii as a food source.

The lack of feeding data for *T. raschii* was the result of the low numbers of this species present in the samples taken for laboratory experiments. In addition, they had a higher mortality rate in the laboratory than *T. inermis*, which meant that with time the replacement animals were all *T. inermis*.

Dry Body Weight and Body Length Relationships

The relationships between dry body weight and total body length, measured from the tip of the rostrum to the end of the telson, were determined for each of the three species. Live animals were measured for length, rinsed in distilled water, dried at 70 C for 72 h, and weighed to the nearest 0.1 mg.

Results

Respiration Rates

The slopes of the respiration equations for each species (Table 1) at different temperatures were compared by an analysis of covariance. Within each of the species there was no significant difference between any of the slopes. The data for different temperatures for each species were pooled, and the pooled data for all species compared by an analysis of covariance. A significant difference was found between the slopes for the different species ($F = 9.62$, df $= 2, 279$, $P < 0.05$). *Meganyctiphanes norvegica* had the lowest slope, while there was no significant difference between the other two species.

The adjusted means of the regression lines of all species were compared by an analysis of covariance. The adjusted means for *M. norvegica* at 10 C were significantly greater than at 5 C. The rate at 5 C measured in the laboratory during July was greater than the 4 C rate measured in the Gulf in June. There was no significant difference between the rates at 4 and 2 C measured in the Gulf in June 1973 and May 1974.

Thysanöessa raschii had a higher respiration rate at 0 C during February than it had at 4 and

TABLE 1. Regression equations for respiration rates of three species of euphausiids measured at different temperatures; $y = \mu l\ O_2 \cdot 24\ h^{-1}$, x = milligrams dry weight, number of data points (N), correlation coefficient (r), and standard error of estimate (SE).

Temp	Equation	N	r	SE	Range of dry wt (mg)	Date	$\mu l\ O_2 \cdot h^{-1} \cdot mg$ dry wt^{-1} for 10 mg animals
		Meganyctiphanes norvegica					
2	$\log y = 2.23 + .35 \log x$	21[a]	.40	.10	34.4– 84.3	Feb. 1973	1.58
2	$\log y = 1.97 + .66 \log x$	48[b]	.55	.12	27.7–125.0	May 1974	1.77
4	$\log y = 1.82 + .69 \log x$	19[b]	.78	.07	32.3–106.7	June 1973	1.35
5	$\log y = 1.97 + .66 \log x$	33[a]	.92	.10	1.5– 53.9	July 1972	1.77
10	$\log y = 1.74 + .96 \log x$	10[a]	.94	.13	2.7– 41.8	Aug. 1972	2.08
		Thysanöessa raschii					
0	$\log y = 1.85 + .81 \log x$	18[a]	.75	.15	2.1– 24.0	Feb. 1973	1.90
2	$\log y = 1.69 + .72 \log x$	39[b]	.75	.12	7.9– 70.0	May 1974	1.70
4	$\log y = 1.62 + .72 \log x$	17[b]	.97	.06	3.0– 18.6	June 1973	1.29
		T. inermis					
0	$\log y = 1.49 + .68 \log x$	9[a]	.79	.15	2.1– 11.0	Feb. 1973	.62
2	$\log y = 1.33 + .98 \log x$	26[b]	.81	.15	8.0– 55.0	May 1974	.85
4	$\log y = 1.37 + 1.16 \log x$	9[b]	.87	.13	6.2– 35.0	June 1973	1.41
10	$\log y = 1.60 + .85 \log x$	17[a]	.86	.13	4.0– 43.1	Aug. 1972	1.17
15	$\log y = 2.08 + .53 \log x$	13[a]	.84	.13	1.4– 33.0	Sept. 1972	1.70

[a]Measured in laboratory.
[b]Measured in the field.

2 C in May in the Gulf. The 4 C rate was significantly greater than the 2 C rate.

Thysanöessa inermis had a significantly higher respiration rate at 15 C in September than at 0 C in February, but no significant difference was found between the rates at the other temperatures.

MOLTING FREQUENCY

A linear relationship was found between the mean number of days between molts and the water temperatures for *M. norvegica* and *T. inermis* (Fig. 1). The calculated regression equations for the two species were:

$$M.\ norvegica\ D = 20.62 - 1.16\ T$$
$$T.\ inermis:\ D = 15.3 - 0.91\ T$$

where D = mean number of days between molts and T = water temperature. The mean dry body weight and standard deviation in milligrams of the animals at each of the temperatures were (numbers in parentheses represent the number of molt periods):

Temp (C)	*T. inermis* (mg)	*M. norvegica* (mg)
0	3.38 ± .58 (18)	—
5	3.65 ± .31 (20)	24.07 ± 7.99 (24)
10	3.41 ± .71 (28)	24.64 ± 14.75 (32)
15	—	28.10 (4)

The larger scatter about the regression line for *M. norvegica* was due to the greater size difference between specimens. The smaller animals generally had a shorter intermolt period at each of the temperatures. Data given by Fowler et al.

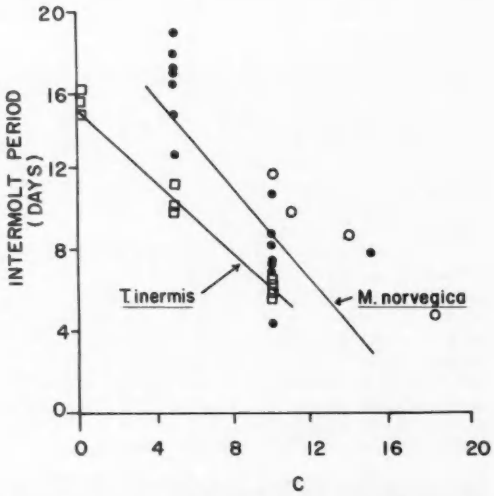

FIG. 1. Intermolt period in days as related to water temperature for *Meganyctiphanes norvegica* and *Thysanöessa inermis*. ●, *M. norvegica*; □, *T. inermis*; and ○, *M. norvegica* taken from Fowler et al. (1971). Each datum point represents the average intermolt period of one animal.

(1971) on the length of the intermolt period and temperature for *M. norvegica* in the Mediterranean Sea are inserted on Fig. 1: The relationship is similar to that found in the present study.

The weights of the dry molts expressed as a percentage of the dry body weight for each species were:

M. norvegica	$6.2 \pm 2.2\%$ ($n = 18$)
T. inermis	$5.7 \pm 1.7\%$ ($n = 15$)
T. raschii	$5.0 \pm 1.0\%$ ($n = 17$)

Feeding Experiments

The number of nauplii added to each beaker was large enough to ensure that <60% of the nauplii were consumed in 24 h.

An experiment was conducted to determine whether the reduced number of nauplii in the beakers after 24 h of feeding affected the number eaten by the euphausiids. This was done by keeping the number of nauplii constant and increasing the volume of water to decrease the density of nauplii. The same euphausiids were used in the experiments at different densities of nauplii. There was no significant decrease in ingestion rate with decreased nauplii density for either *M. norvegica* or *T. inermis* (Table 2).

The relationships between dry body weight, calories ingested, and the respiration rate at different temperatures are given in Table 3. The number of calories used in respiration related to calories ingested increased with increasing body size, reaching over 100% of the number of calories ingested in the case of the largest specimens. This may have indicated that the nauplii were not a suitable source of food for the largest animals. Large numbers of nauplii remained in the beakers after 24 h of feeding by these large animals. The reason more nauplii were not eaten is unknown.

The number of calories ingested, expressed as a percentage of the total calories in the body of the euphausiid (I cal/B cal × 100) decreased with increasing body size and decreasing water temperature. The regression lines relating percentage of body calories consumed to dry body weight (Table 4) were compared by an analysis of covariance. There was no significant difference between the slopes of the lines for either species. The adjusted means were compared by an analysis of covariance. The mean I cal/B cal at 0 C for *T. inermis* was significantly lower than at 5, 10, or 15 C ($F = 20.98$, df = 1, 24, $P < .05$). There was no significant difference between the adjusted means for I Cal/B Cal at 5, 10, and 15 C.

The adjusted means for I Cal/B Cal at 10 and 15 C for *M. norvegica* were not significantly different at $P < .05$, but the 5 C value was significantly lower than the 10 and 15 C values (5 C vs. 10 C, $F = 46.3$, df = 1, 5; 5 C vs. 15 C, $F = 196.30$, df = 1, 4, $P < .01$).

The number of calories ingested relative to total body calories was greater in *M. norvegica* than in *T. inermis* for animals of the same size.

The respiration data for *M. norvegica* at 15 C was taken from Mauchline and Fisher (1969). The value of 0.43 μl $O_2 \cdot mg^{-1}$ wet $wt \cdot h^{-1}$ was used to calculate the number of calories used in respiration. This gave lower values for respiration than were measured at 10 C. This may have been due to the value of 0.43 μl O_2 representing the resting rate which was estimated by Teal and Carey (1967) to be one third of the active rate. The respiration rates in this study were probably closer to the active rate, for the animals appeared to be constantly swimming while in the experimental bottles.

Table 2. Number of nauplii eaten in 24 h at different densities. Experiments were run at 5 C.

No. of nauplii · ml^{-1}	Vol of container (*ml*)	Mean no. eaten ±SD
	M. norvegica	
0.5	2000	110±53[a]
1.0	400	148±52[a]
2.2	200	175±69[a]
	T. inermis	
0.04	5000	97±46[b]
0.1	2000	95±34[b]
0.3	800	92±30[a]

[a]Based on 15 days of observations.
[b]Based on 10 days of observations.

Energy Consumption in the Environment

In 1973 three surveys were made in the upper estuary of the Gulf of St. Lawrence to locate concentrations of euphausiids using high frequency sonar (Sameoto 1972, 1976; Sameoto and Jaroszynski 1973). Using the data collected during these surveys in June, September, and December 1973, it was possible to estimate the size of the euphausiid populations in this region. Zooplankton samples taken at these times gave data on the body sizes of the three species present.

The total body lengths of animals in the populations of *M. norvegica* and *T. raschii* are shown in Fig. 2. The dry body weight and total body length relationships were determined for each species and the regression equations were used to calculate the mean dry body weight of the populations. The regression equations are (TL =

TABLE 3. Results of feeding experiments at different temperatures showing relationship between calories of respiration calculated from regression equations (Table 1) and ingestion.

Dry wt (*mg*)	No. cal eaten $\bar{x}$	± SD	Cal used in resp·24 h^{-1}	Cal in resp / Cal eaten × 100	Days of observations
			T. inermis		
			15 C		
8.10	3.92	1.08	1.84	47	20
13.80	2.73	0.32	2.36	86	20
13.80	2.51	0.82	2.35	94	25
16.80	5.15	1.12	2.55	49	21
24.70	5.20	0.74	3.05	59	26
			10 C		
10.30	2.13	0.62	1.30	61	20
16.20	2.13	0.38	1.99	93	20
17.60	2.98	0.56	2.12	71	29
26.60	2.73	0.78	3.10	113	20
35.70	2.69	.26	4.07	151	15
			5 C		
2.00	1.78	.78	.25	14	24
3.10	2.93	.92	.42	14	25
3.50	1.48	.37	.48	33	20
3.60	1.54	.42	.50	32	25
3.88	2.42	.87	.53	22	25
8.50	2.82	.81	1.35	59	25
9.50	2.88	1.05	1.07	37	25
11.00	3.54	1.04	1.82	52	25
			0 C		
2.00	1.60	.62	.23	15	25
3.10	1.81	0.84	0.35	19	30
3.13	0.63	.29	.32	51	30
3.13	0.62	.33	.32	52	25
8.50	0.88	.58	.63	72	30
9.50	1.33	.36	.77	58	30
11.00	1.30	0.46	.75	58	30
17.00	1.54	.61	1.00	65	27
21.90	1.25	0.26	1.16	93	28
23.80	1.36	0.3	1.27	93	30
			M. norvegica		
			15 C		
1.67	4.22	1.31	.44[a]	10	10
1.90	3.93	0.04	.47[a]	12	15
2.27	4.19	0.11	.56[a]	13	14
2.52	3.84	0.07	.62[a]	16	15
3.46	5.56	0.49	.92[a]	17	12
			10 C		
1.30	2.62	0.70	0.84	32	25
1.54	3.47	0.74	0.95	27	25
1.92	2.71	0.66	1.10	40	25
2.69	3.00	0.68	1.40	47	24
4.34	4.86	1.15	1.96	40	25
19.10	7.81	2.47	5.53	71	20
29.90	16.41	0	7.17	44	25
53.80	13.43	0	10.93	81	25
			5 C		
1.48	1.28	0.62	0.64	50	25
1.80	1.63	0.36	0.72	44	25
2.31	1.73	0.89	0.84	48	25
2.47	1.47	0.96	0.88	60	25
35.83	2.92	1.88	4.89	1.67	25

[a]Calculated from Mauchline and Fisher 1969.

TABLE 4. Regression equations relating dry body weight in milligrams (x) to percentage of total body calories ingested (y).

Temp	*M. norvegica*	*T. inermis*
15	$\log y = 1.79 - .61 \log x$	$\log y = 1.47 - .66 \log x$
10	$\log y = 1.65 - .52 \log x$	$\log y = 1.45 - .80 \log x$
5	$\log y = 1.39 - .70 \log x$	$\log y = 1.42 - .63 \log x$
0		$\log y = 1.28 - .91 \log x$

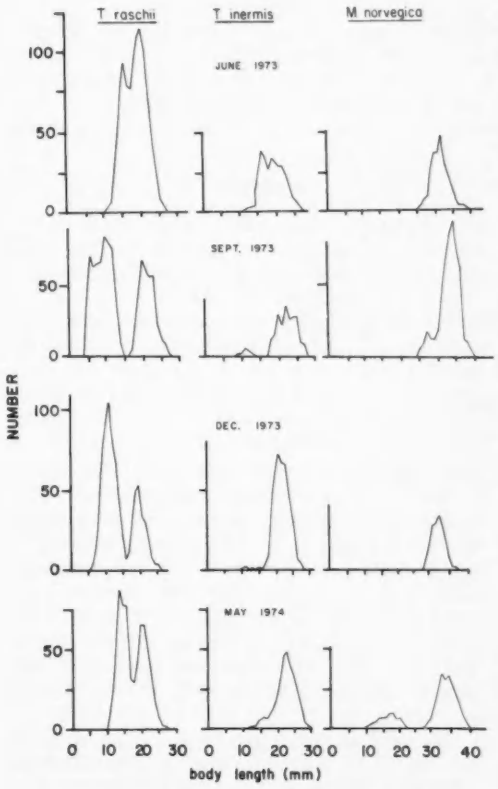

FIG. 2. Distribution of total body length (measured from tip of rostum to the end of the telson) of three species of euphausiid found off the coast of Gaspé.

total length):

	No. data points	Length range (*mm*)
M. norvegica Body wt = $.00029\ TL^{3.50}$	(58)	6–41
T. raschii Body wt = $.000717\ TL^{3.17}$	(40)	10–24
T. inermis Body wt = $.000712\ TL^{3.38}$	(62)	18–30

Using these conversions the dry weight for the average euphausiid in the three populations was calculated (Table 5). These values and the relationship between number of calories ingested and dry body weight made it possible to estimate the minimum number of calories the average euphausiid would ingest in 24 h. This was done for all three species for each of the three sampling periods (Table 5).

The high frequency sonar survey during June 1973 in the Gaspé region of the Gulf found sound-scattering layers caused by euphausiids over an area estimated to be 4375 km^2 (Sameoto and Jaroszynski 1973; Sameoto 1976). The average number of euphausiids was estimated at 200 m^{-2}. The percentages of the three species in the population were 65% *T. raschii*, 24% *T. inermis*, and 11% *M. norvegica*.

The estimated total consumption for all species of euphausiids was 602 cal·m^{-2}·day^{-1}. Steven (1974) estimated the primary production during June and July in the Gaspé current, the area of the sonar surveys, to be 2.88 g·m^{-2}·day^{-1} or an equivalent of 38.30 kcal·m^{-2}·day^{-1} using Vollenweider's (1965) conversion. The estimated consumption in calories per square meter per day by the euphausiids for June was 1.5% of the primary productivity. Gut examinations of the three species caught in June showed that they fed primarily on phytoplankton with lesser amounts of small zooplankton. This agreed with the findings of Berkes (1973).

The mean water temperature the animals were exposed to during 24 h in June was 2.25 C, which meant that the *M. norvegica* molted once in 18.01 days and *T. inermis* and *T. raschii* once in 13.25 days. I assumed that *T. raschii* molted at the same frequency as *T. inermis*. *Meganyctiphanes norvegica* made up 40% of the biomass of the population and the other two species 60%. The estimated weight of molts produced by each species is given in Table 5. The total population of euhpausiids produced 12.6 mg of molts·m^{-2}·24 h^{-1} in the region of the heavy concentrations of euphausiids. Lasker (1966) found the molts of *Euphausia pacifica* contained 17.0% carbon. By using this figure it was estimated that euphausiids in the Gulf shed 2.14 mg C·m^{-2}·24 h^{-1} during June. The *M. norvegica* population lost 3.0% of its total carbon due to molts every 18 days and the *T. raschii* and *T. inermis* populations lost 2.5% and 2.9% of their total carbon,

TABLE 5. Mean dry body weight of the species of euphausiids found in the Gulf of St. Lawrence estuary during the three sampling periods in 1973.

Date (1973)	Mean dry wt[a] ± SD (*mg*)	% total body cal ingested	Cal ingested · animal^{-1} · day^{-1}	No animals · m^{-2} in heavy sound scattering layers	Cal consumed · day^{-1} · m^{-2}	mg molts · m^{-2} · day^{-1}[b]
			M. norvegica			
June	61.9±16.5	1.37	4.29	22	94	4.7
Sept.	65.1±13.2	1.32	4.34	—	—	—
Dec.	58.2±15.6	1.43	4.21	—	—	—
			T. inermis			
June	13.2±11.1	5.20	2.22	48	107	2.7
Sept	18.1±11.1	4.40	3.90	12	47	0.3
Dec.	22.8±11.9	3.92	4.39	—	—	—
			T. raschii			
June	10.6± 5.1	5.90	3.10	130	403	5.2
Sept.	0.8± 0.3[c] 11.5± 1.2[c]	16.58[d]	1.24[d]	1168	1446	25.9[d]
Dec.	1.9± 0.4[c] 11.5± 1.2[c]	8.01[d]	2.17[d]	880	1909	14.0[d]

[a]1 g dry wt of *M. norvegica* = 5.06 kcal; 1 g dry wt of *T. inermis* = 4.91 kcal; 1 g dry wt of *T. raschii* = 4.95 kcal.

[b]$$\text{mg molts m}^{-2}\,\text{day}^{-1} = \frac{\text{mean body wt} \times \text{no. animals} \cdot \text{m}^{-2} \times \frac{\text{molt wt}}{\text{body wt}} \times 100}{\text{days between molts}}.$$

[c]Mean dry weight of separate population modes (See Fig. 2).
[d]Weighted mean of the two modes.

respectively, every 13.25 days as a result of molting. Clutter and Theilacker (1971) found the calorific content of the whole molt of the mysid *Metamysidopsis elongata* to be 2.98 cal·mg^{-1} dry wt. If the value for the euphausiid molts is similar, the euphausiid population shed 37.55 cal·m^{-2}·24 h^{-1} or 6% of the calories ingested in 24 h.

In September the area containing dense concentrations of euphausiids was confined to two small areas near the eastern tip of Gaspé with a total area of 400 km^2 (Sameoto 1976). The density of euphausiids in these areas was estimated at 1180 animals·m^{-2}. The population consisted of 99% *T. raschii*, about 60% of which were juveniles (Fig. 2). These animals migrated to the top 10 m of water during the night and remained there for about 6 h. The water temperature of this layer averaged about 10 C. During the day the animals remained at a depth of 100–150 m in water of 0 C. The energy requirements were calculated separately for the two population modes, assuming *T. raschii* and *T. inermis* had similar energy requirements. The first mode (Fig. 2) represented 63% of the population with a mean dry body weight of 0.8 mg, and the second mode represented 37% of the population with a mean body weight of 11.5 mg. The first mode was estimated to have consumed 716 cal·24 h^{-1}·m^{-2} and the second 730 cal·24 h^{-1}·m^{-2}, which meant the total population, by spending 6 h at 10 C and 18 h at 0 C, would have had to ingest 1.446 kcal·m^{-2}·24 h^{-1} to meet its minimum energy requirements. The estimated primary production in the region in September was 0.38 g C·m^{-2}·24 h^{-1} (Steven 1974), or 5.05 kcal; therefore, the euphausiids in areas of high density consumed about 29% of the primary production.

The animals were exposed to a mean temperature of 5 C; therefore, the average intermolt period was 10.7 days. Fowler et al. (1971) found the intermolt period of euphausiids exposed to fluctuating temperatures was the same as that for animals exposed to the average temperature for the same period. Hence, the total quantity of molts produced was 25.9 mg^{-1}·m^{-2}·24 h^{-1} or 77.18 cal·m^{-2}·24 h^{-1}. This represented 1.9% of the calories consumed daily by the population in the areas of high density.

In December the water temperature was uniform at 0 C from the surface to 150 m. The euphausiid population in the heavy scattering layers, which covered an area similar to that of September, was 100% *T. raschii*. The heavy scattering layers had densities of 880 animals·m^{-2}.

The first mode (Fig. 2) represented 69% of the population with a mean body weight of 1.9 mg and the second 31% with a mean body weight of 11.5 mg. Using the same weighted procedure as for the September data it was calculated that the population consumed 1909 cal·m^{-2}·24 h^{-1} (Table 5). The intermolt period at 0 C was estimated to be 15.3 days. The population in the dense scattering layers therefore produced 14.0 mg of molts·m^{-2}·24 h^{-1}, of 41.7 cal of molts·m^{-1}·24 hr^{-1}. This represented 2.2% of the calories ingested daily. The estimated primary production in December was 0.24 g C·m^{-2}·24 h^{-1} (Steven 1974), or 3.192 kcal·m^{-2}·24 h^{-1}. The euphausiids consumed about 60% of the primary production in 24 h.

Discussion

The euphausiids in the upper estuary of the Gulf of St. Lawrence were exposed to a narrow temperature range from December to June (0–4 C), but in September their daily vertical migrations exposed them to temperatures from 0 C (below 25 m) to 14 C near the surface. It was demonstrated that each of the species had different respiration rates at the same temperature in these studies. *Meganyctiphanes norvegica* had the highest rate and *T. inermis* the lowest respiration rate. Both *M. norvegica* and *T. raschii* were apparently able to acclimate to temperature changes so as to stabilize their respiration rates. This was evidenced by similar rates at 2 and 5 C for *M. norvegica* and the higher rate at 0 than at 4 C for *T. raschii*. *Meganyctiphanes norvegica* had a higher respiration rate than *T. inermis* at all temperatures tested. This probably explains why *M. norvegica* had a higher I cal/B cal ratio at 15 and 10 C than *T. inermis* at these temperatures.

Artemia nauplii may have been a poor source of food for the large specimens of both species of euphausiid. This was indicated by the ratio of calories ingested and the amount used in respiration which showed that some animals used more energy in respiration than they ingested (some large specimens exhibited no growth or negative growth between molts). The larger animals may have been more active in the respiration bottles than smaller animals and thereby gave abnormally high values for the respiration rates compared with the rates in the feeding beakers. The small specimens showed some growth between molts, but the animals were not kept long enough to obtain a growth rate.

The estimated energy consumption of euphausiids in the Gulf may have been underestimated. The assimilation rate of animal matter such as the *Artemia* nauplii may be different from the assimilation of phytoplankton on which the animals primarily feed in the Gulf. Generally, carnivores have a higher assimilation rate than herbivores and detritivores (Welsh 1968). Therefore, the percentage of the primary production ingested by the euphausiids in the Gulf may be higher than the values estimated from the experimental ingestion rates.

The contribution of the molts to detritus in the Gulf was less than that estimated by Lasker (1966) for *Euphausia pacifica* in the Pacific Ocean. He stated that the molts may have totaled 7 times the euphausiid biomass. This was based on a value for molts of 10% dry body wt and a molting frequency of 5 days. Berkes (1973) estimated a euphausiid molt remained intact for 5 or more days at 5–6 C and settled at a rate of 180 m·24 h^{-1}. Therefore, all the molts in the Gaspé region would have reached the seabed if not attacked by zooplankton. This represented about 129 mg C·m^{-2} added to the seabed during the 61 days of May and June when the population of euphausiids in the area was at its peak.

Extrapolating experimental results dealing with feeding and respiration rates to natural field populations should be done with caution because we do not understand the effects of the stress of capturing and handling the animals under experimental conditions. The reaction of the animals to the boundaries of the holding container and the constant stimulation of the animals from unavoidable vibrations of equipment all likely influence the animals physiology in unknown ways. The physiological and behavioral effects of the animals being fed an unnatural food such as *Artemia* larvae are unknown, but must be important as evidenced by the lack of growth by the larger specimens of euphausiids. Other uncertainties arose from lack of information on the natural environment of the animals. It is known that the euphausiids migrate vertically each night from midwater, 150 m, to the upper 25 m (Şameoto 1976). The guts of these animals contained a green amorphous material that showed remnants of algal cells, and a large amount of unidentified material. It is probable that small zooplankters and detritus were also eaten as well as the phytoplankton. The amount of energy obtained from zooplankton relative to phytoplankton is unknown.

Various attempts have been made to estimate the active swimming metabolism of zooplankton in the natural environment and it is generally assumed to be 2–3 times the standard metabolism. Klyashtorin and Yarzhombek (1972) cal-

culated that slow vertical migration of zooplankters such as euphausiids would only require a 20–30% higher energy expenditure than standard metabolism; therefore, I conclude that the field respiration rates differed little from the standard metabolism measured in the laboratory.

Since we have no direct measurements of the respiration and feeding rates in situ for these animals we must rely on measurements made in the laboratory. When these data are handled with care they can provide reasonable approximations of events in the real world and a valuable base for future studies in the field and laboratory.

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Fin Erosion Disease of Starry Flounder (*Platichthys stellatus*) and English Sole (*Parophrys vetulus*) in the Estuary of the Duwamish River, Seattle, Washington[1]

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Fin erosion in the starry flounder (*Platichthys stellatus*) and English sole (*Parophrys vetulus*) of the Duwamish River, Washington, is characterized by ulcerating chronic inflammation and fibrosis with resorption of fin rays. The end result is deformation, shortening, and retraction of residual fin tissue with loss of functional surface. We suggest that the incidence of fin erosion in a particular population is related to an interaction between genetic constitution and multiple environmental variables, including a variety of chemical pollutants.

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L'érosion des nageoires du cardeau étoilé (*Platichthys stellatus*) et de la sole anglaise (*Parophrys vetulus*) de la rivière Duwamish, Washington, est caractérisée par une inflammation chronique ulcérative et une fibrose accompagnée d'une résorption des rayons des nageoires. Le résultat final est une déformation, un rétrécissement et une rétraction du tissu résiduaire de la nageoire, avec perte de surface fonctionnelle. L'occurrence de l'érosion des nageoires dans une population particulière serait liée à une interaction entre la constitution génétique et plusieurs variables du milieu, y compris divers polluants chimiques.

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FIN erosion disease (or fin rot) is a progressive destruction of fin tissue observed in a number of species of freshwater and marine fish. The disease may be acute with ulceration and necrosis or more chronic with epidermal hyperplasia and dermal fibrosis. Although the etiology is unknown, certain bacterial and chemical agents are strongly implicated (Davis 1953; Sindermann and Rosenfield 1954; Oppenheimer 1958; Bullock 1968; Amlacher 1970; Bullock and Snieszko 1970; Levin et al. 1972; Mahoney et al. 1973; Mearns and Sherwood 1974; Ziskowski and Murchelano 1975). Fin erosion has recently been reported in several species of the family Pleuronectidae (flounders, flatfish) at two coastal locations, one on the east coast, and one on the west coast of the United States.

On the east coast epizootics of fin erosion were observed annually from 1967 to 1973 in marine and euryhaline fishes in the New York Bight (Mahoney et al. 1973). The highest incidence was observed at the apex of the Bight which receives waters bearing heavy concentrations of domestic and industrial pollutants (Ziskowski and Murchelano 1975). Species involved were the winter flounder (*Pseudopleuronectes americanus*), the summer flounder (*Paralichthys dentatus*), and to a lesser extent, the windowpane (*Scophthalmus aquosus*). Ulcerating lesions were characterized by necrosis, exposure of fin rays, and loss of fin tissue; other lesions showed marked fibrosis and epidermal hyperplasia.

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A similar if not identical disease was observed in Dover sole (*Microstomus pacificus*) (Klontz and Bendele 1973; Mearns and Sherwood 1974) collected in southern California coastal waters in the vicinity of major municipal sewage outfalls. Acute lesions showed fraying of fins with denuding of the tips of the fin rays. With further progression the bony rays degenerated and the fin thickened due to proliferation of fibroblasts and collagenization of the dermis between and around the fin rays. There was aggregation of melanophores along the edges of the eroded fins.

Fin erosion was also reported by Salo (1969) in starry flounder (*Platichthys stellatus*) from the Duwamish estuary, Washington, but without pathological description. The present report documents the pathology and prevalence of fin erosion disease in the starry flounder and in the English sole (*Parophrys vetulus*) from the estuary and lower portion of the Duwamish River.

Materials and Methods

Collections were made during 1974 and the first 9 mo of 1975 in the Duwamish River, at eight collecting stations (A–H) in the lower river and estuary (Fig. 1). This portion of the river is lined by ship moorages and industrial facilities. Single 5-min hauls were made monthly at each station by means of an otter-trawl with 6-mm mesh in the codend, operated from a 5-m Boston Whaler equipped with mast, boom, winch, and wire for trawling in shallow water. The separate catches were iced in the field and returned to the laboratory for processing which included identification by species, enumeration, measurement for total length (millimeters), and examination for fin erosion and other diseases.

Specimens of skin lesions for histopathology were fixed in the field in phosphate-buffered 10% Formalin with 0.85% NaCl. After fixation the tissues were blocked, embedded in paraffin, sectioned at 6 μm, and stained with hematoxylin and eosin (H&E). Control skin was taken from 38 normal fish from West Point in northwest Seattle and from previous collections made in East Sound of Orcas Island, Washington. In some instances, special stains including periodic acid-Schiff (PAS), Oil red O for neutral fat, Giemsa, Van Giesen, Ziel-Nielsen, Gram, mucicarmine, and Schorr's stain for inclusion bodies were employed utilizing standard techniques.

Results

A total of 6547 fish of 29 species was collected in 1974. Fin erosion was observed only in the starry flounder and English sole. The incidence by month of fin erosion in starry flounder ranged from a low of 1.6% in July to a high of 14.6% in March with an average incidence of 8% (Fig. 2a). The monthly incidence of fin erosion in English sole was lower, averaging 0.5%. Fin erosion was observed at stations B–H, indicated on the map (Fig. 1), but the incidence varied at the different stations (Fig. 2b). The differences were not considered significant because of the small size of some of the samples.

Gross Pathology

Fin erosion in the starry flounder and English sole most frequently affects the dorsal and anal fins; the caudal fin is occasionally involved, and rarely the pectoral and pelvic fins (Table 1, Fig. 3). There is no difference in the frequency of fin erosion on the pelvic fins of the eyed side vs. the blind side. However, pectoral fins of the blind side are more often diseased than the pectoral fin of the eyed side.

The lesions of fin erosion vary from minor defects to extensive destruction of fins (Fig. 3–6). Sometimes almost entire fins are destroyed (Fig. 3). In the less severe lesions there is partial loss, fusion, or distortion of fin rays, generally accompanied by hemorrhages and granulation tissue on the surface of the fin and extending to the main body surface (Fig. 4). Slight to moderate ulceration may be seen at the free margin of the damaged fin, which is often greatly scarred. There is usually a line of hyperpigmentation along the free edge of the defect (Fig. 4, double arrows).

In the most severe lesions parts of the fins have lost the bony fin rays entirely and the remaining soft tissue is greatly scarred, retracted, flaccid, and deformed (Fig. 6). The flat epithelial surfaces of such fins are generally without ulceration, but there may be ulceration at the free margin. Frequently, flaps of unsupported fin tissue are folded over so as to graft themselves by permanent tissue union to the adjacent body wall.

Histopathology

The lesions we observe in starry flounders and English sole are largely those of a chronic fibrosing disease with epidermal hyperplasia, proliferation of dermal fibroblasts, fibrosis, focal infiltrations of cells interpreted as lymphocytes, mucous cell changes, aggregation of melanophores in the vicinity of resorbing fin rays and around sclerotic blood vessels, patchy loss of melanophores from the dermal–epidermal junction, and an increase and spreading of eosinophilic granular cells in the epidermis (Fig. 7–14). These and some other changes are described in the following paragraphs. The majority of lesions are a composite of most if not all of the features described.

Epidermal hyperplasia is a constant feature of

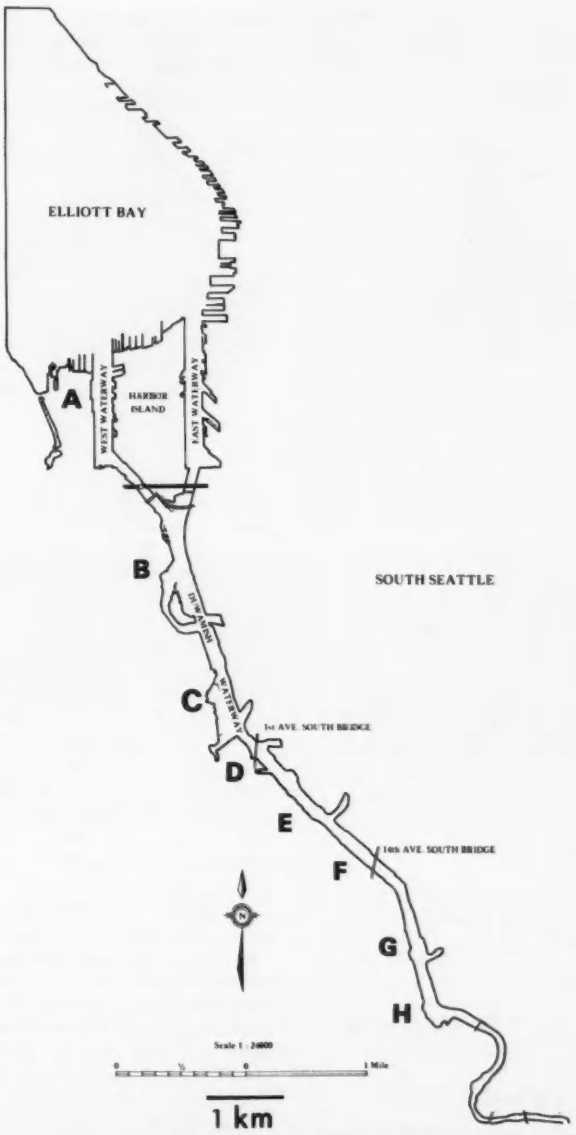


FIG. 1. Lower industrialized portion of the Duwamish River and Elliot Bay showing collecting sites (A–H).

the disease. The normal epidermis of the fins of starry flounders and English sole is 7–10 cells thick. The basal layer consists of small germinal cells with basophilic nuclei. As the progeny of the basal cells progress toward the surface they differentiate into flattened squamous cells, or mucous cells, or eosinophilic granular cells (EGC). In our specimens there is hyperplasia of the epidermis to 2–3 times the normal complement of cells with a corresponding increase in thickness. The individual epidermal cells are generally of normal morphology, but focal fraying of the epithelium, accompanied by degenerative changes in the individual cells, may be seen. Mild

TABLE 1. Occurrence of fin erosion disease by fin on individual starry flounder (*Platichthys stellatus*) collected from the Duwamish River during 1974 (all stations and months combined). No sampling was conducted during October.

	Dorsal	Anal	Caudal	Eyed pectoral	Blind pectoral	Eyed pelvic	Blind pelvic
Jan.	21	14	6	0	2	3	3
Feb.	16	7	5	2	8	1	1
Mar.	18	10	6	3	6	5	5
Apr.	14	16	7	0	2	0	0
May	4	0	1	1	1	4	4
June	2	2	1	0	0	0	0
July	2	1	2	0	0	1	1
Aug.	3	1	5	0	0	0	0
Sept.	3	3	4	1	1	1	1
Nov.	2	2	1	0	0	0	0
Dec.	3	3	1	0	1	0	0
Total	88	59	39	7	21	15	15

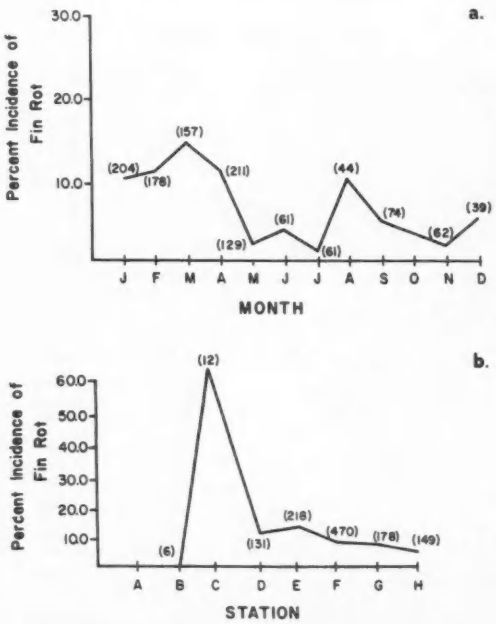


FIG. 2. Percent incidence of fin erosion on starry flounder (*Platichthys stellatus*) a, by month and b, station, during 1974. Total number of fish with fin erosion for the year is indicated in parentheses.

papillary folding of the epidermis and underlying dermis is often present (Fig. 7).

Ulceration of the epidermis with necrosis and exfoliation of small strips of epithelium may be present (Fig. 9–11). These are often detected only microscopically and in no way represent massive necrosis. Granulation and scar tissue are present in the bases of the ulcerations.

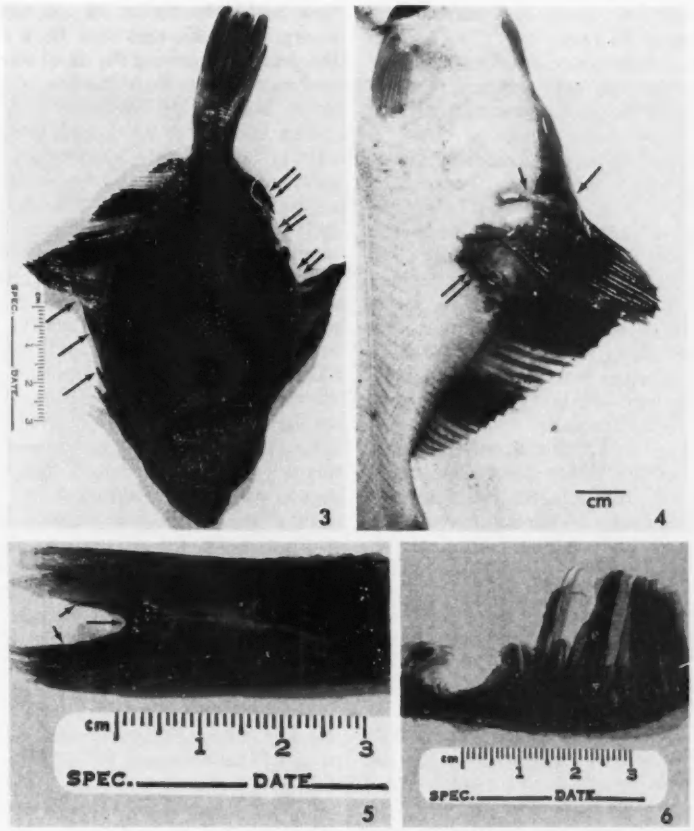
Areas of hyperplasia of mucous cells (Fig. 8) alternating with areas of decrease or absence (Fig. 7) are observed in the epidermis of affected fins. Under normal conditions mucous cells are evenly distributed throughout the epidermis. The mucous droplets in the cells stain with mucicarmine, and PAS reaction is positive, indicating the presence of mucopolysaccharide.

There is hyperplasia of eosinophilic granular cells (EGC) in the epidermis. The EGC are found normally only in the inner layers of the epidermis just above the basal layer. In fin erosion, EGC are not only increased in numbers but are scattered diffusely throughout the full thickness of the epidermal layers (Fig. 10).

Inclusion cysts lined by epidermal or mucous cells and solid epidermal inclusions are often observed in severely damaged skin. This change usually occurs in fins where the bony rays are largely resorbed, resulting in loss of tissue support. The distal fin may then fold back on the more proximal portion or on the body wall, resulting in entrapment of epithelial sheets. As the tissue heals in this position, inclusion cysts may form (Fig. 9 and 10).

Proliferation of fibroblasts and marked fibrosis of the damaged fin is a constant feature of fin erosion. The fibrosis is accompanied by sclerosis of small blood vessels in the central vascular axis of the fin web. There is also perineural fibrosis involving the small peripheral nerves (Fig. 7 and 10).

Under normal conditions melanophores are evenly spaced along the inside of the dermal–epidermal junction. In fin erosion there is a



FIGURES 3–6

FIG. 3. Starry flounder with fin erosion of the anterior half of the anal fin (left lower portion of photograph, single arrows) and the posterior half of the dorsal fin (right upper portion of photograph, double arrows). Much of the unsupported soft tissue of the posterior half of the dorsal fin is folded over so as to graft itself to the adjacent body wall. FIG. 4. Appearance of moderate fin erosion of anal fin of starry flounders. The anterior part of the fin (upper part of photograph) shows collapse of fin rays, loss of tissue, and grey opacity due to fibrosis. The damaged tissue is folded (single arrows). A patchy zone of pigmented scar tissue spreads out over the adjacent body wall (double arrow). FIG. 5. Eroded caudal fin of starry flounder with central notch (arrows) due to loss of distal soft tissue and portions of central fin rays. Grey central opacity is due to scar formation with folding and retraction. FIG. 6. Severe fin erosion of English sole (*Parophrys vetulus*). This portion of the dorsal fin was cut from the body wall. The free edge is above. Note irregular ulceration of soft tissue and fin rays.

change in distribution of the melanophores and possibly also an absolute increase in numbers. At the dermal–epidermal junction melanophores may be focally decreased in numbers or absent, or they may be crowded and focally increased (Fig. 10 and 11). Melanophores are also regularly distributed through the deeper fibrocollagenous tissue where they are rarely found. They are often perivascular and perineural in location. Melanophore concentrations are greatest in the

proliferative fibroblastic areas and surrounding foci of absorption of fin rays.

Melanophages (macrophages that have phagocytozed melanin granules or fragments of cytoplasm of melanophores) are sometimes present in the fibrocollagenous scar.

Resorption of fin rays is a constant feature of fin erosion. Figure 12 is a longitudinal section of a normal fin ray and a fin ray that has been completely resorbed and replaced by fibroblastic tissue and collagen. The resorptive process (Fig. 13) involves basophilic cells closely spaced along the surface where resorption is taking place. Most of these cells have one or sometimes two nuclei; there are no large multinucleated cells suggestive of the familiar mammalian osteoclasts. The resorptive process often involves the two spicules of the fin ray unequally.

Infiltrations of mononuclear cells interpreted as histiocytes and small lymphocytes are scattered focally through the scar tissue of the deformed fins. Multiple stains for pathogenic organisms in tissue (see Materials and Methods) are negative.

Discussion

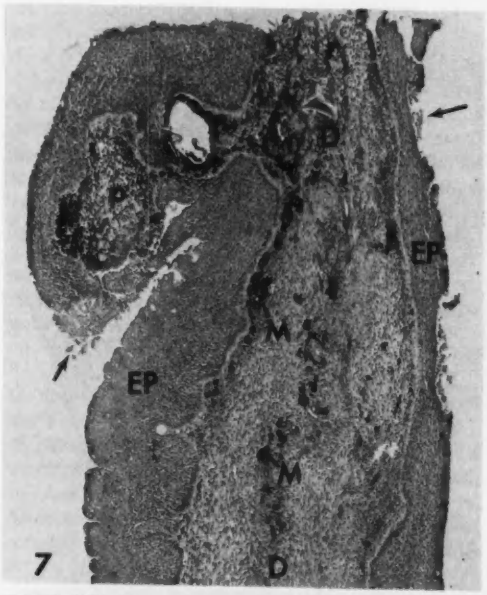
Our work generally agrees with previous studies of fin erosion in other species (Levin et al. 1972; Klontz and Bendele 1973; Mahoney et al. 1973; Mearns and Sherwood 1974; McDermott and Sherwood 1975; Murchelano 1975). The dorsal and anal fins are most frequently involved and the histopathology of the tissue lesions is similar. Other descriptions also mention focal zones of ulceration at the distal (free) margin of the affected fins, accompanied by extensive subacute and chronic fibrosing inflammation of the underlying connective tissue. We believe that these changes are fundamental and directly related to the scarring, retraction, and deformation of the affected fin. The resorption of fin rays may be a crucial part of the process, depriving the fin of structural support and accentuating the refraction, shortening, thickening, and loss of functional surfaces.

The etiology of fin erosion is unknown. Davis (1953) believes that in salmonids the disease is most commonly caused by bacteria, but other agents may be involved. Other authors (Snieszko 1958; Bullock 1968; Bullock and Snieszko 1970) implicate myxobacteria as possible etiological agents. In some other diseases, such as bacterial dermatitis, similar pathology may be noted (Sindermann 1966). Schaperclaus (1950) isolated bacteria of the genera *Aeromonas* and *Pseudomonas* from black mollies affected by fin rot. Apparently, a variety of bacteria have been suggested as etiological agents in the instance of salmonids and other fishes. In this regard it is always difficult to distinguish primary etiological agents from secondary (opportunistic) invaders.

In marine fishes *Pseudomonas* can induce experimental fin rot in the cod *Gadus callarius* (Oppenheimer 1958). In the herring *Clupea harengus*, gram-negative, nonspore-forming pleomorphic rods were isolated from the ulcerated surface lesions, as well as from blood, kidneys, and skeletal muscle of affected fish (Sindermann and Rosenfield 1954).

The studies of Mahoney et al. (1973) implicate *Aeromonas*, *Pseudomonas*, and *Vibrio* in pleuronectids. These authors believe that the two conditions of dense pathogenic bacterial populations and environmental stress are prerequisites for the occurrence of the epizootic in the New York Bight. Pollution by domestic, agricultural, and industrial wastes could provide the high bacterial density and the environmental stress in the form of multiple harmful chemical agents. The chemi-

FIG. 7 Histologic appearance of lesion seen in Fig. 6. Cross section of fin shows variable degrees of epidermal hyperplasia to right and left (EP). The dermal tissue (D) in the center shows fibrosis, uneven distribution of melanophores (upper M) along the dermal–epidermal junction, increased melanophores (lower M) centrally and localized around nerves and blood vessels. There are zones of focal necrosis and exfoliation of epithelium (arrows). Fin rays are completely resorbed and resultant soft tissue changes include epithelial folding and development of dermal papilla (p) projecting into epidermis. H&E; 64×. FIG. 8. Section through part of folded and distorted fin from a starry flounder showing increased numbers of mucous cells (M) and darkly staining eosinophilic granule cells (EGC). H&E; 64×. FIG. 9. Diseased fin from English sole with focal zones of acute epidermal ulceration (arrows); fin rays (FR) with resorption of parts of the bony portions; and inclusion cysts lined by squamous cells (SC) and by mucous cells (MC). The dermal stroma shows marked fibrosis and irregular distribution of very dark melanophores. H&E; 34×. FIG. 10. Fin erosion in English sole. Epidermis is hyperplastic and there are numerous eosinophilic granular cells (EGC), visible as tiny individual dark spots at this power. Note irregular distribution of very large melanophores (M) at the dermal–epidermal junction and around blood vessels and nerves. The dermis is very fibrotic and sclerosis of blood vessels (arrow) and perineural fibrosis are apparent (double arrow). H&E; 85×.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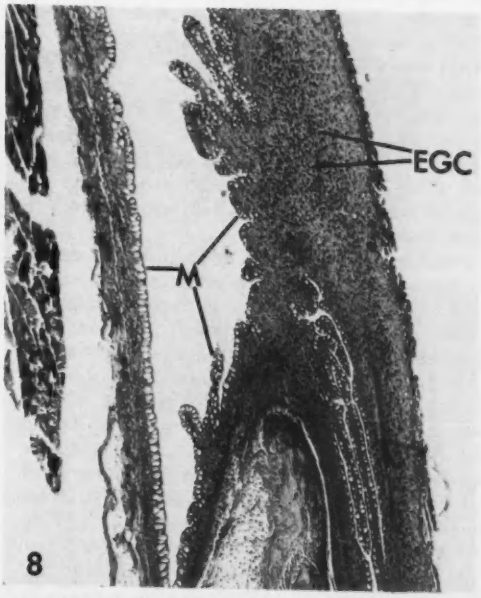
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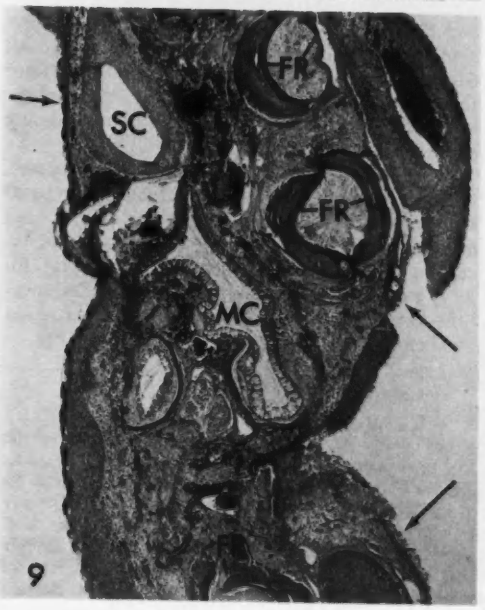
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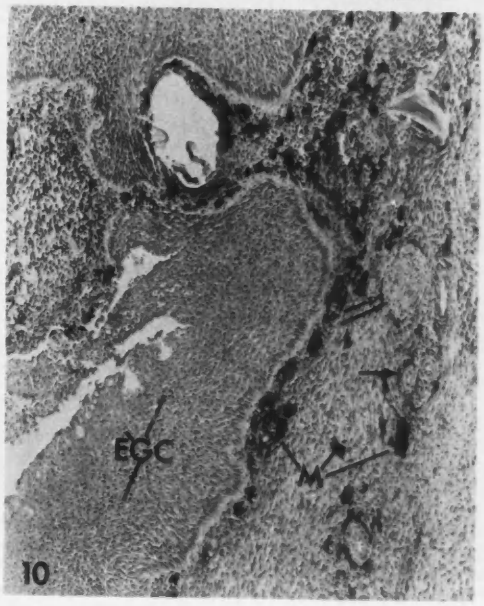
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cal agents could include heavy metals, polychlorinated biphenyls (PCB), insecticide residues, herbicides, and household detergents.

In this regard McDermott and Sherwood (1975) determined levels of PCB and DDT in Dover sole (*M. pacificus*) without the fin erosion from the Palos Verdes area of the Southern California Bight. They found that Dover sole with fin erosion had slightly higher, but not statistically significant, levels of PCB than did normal Dover sole. DDT was found to be consistently and significantly higher in fish with fin erosion than in those without.

Analyses of PCB levels in English sole of the Duwamish River have been performed biannually since 1972 by the Environmental Protection Agency in cooperation with the Washington State Department of Fisheries. Levels of both Aroclor® 1260 and 1254 consistently averaged 1500 ppb (dry wt) for total body mass (Pattie 1975). Fish from five other estuaries of Puget Sound and the Washington coast did not have detectable PCB concentrations. PCB analyses of livers from starry flounders captured in the Duwamish River have also detected abnormally high levels of PCB (5.2 ppm, wet liver wt) (Pavlou 1973).

A probable continuous source of PCB in the Duwamish River is the bottom sediments. In analyses of such sediments performed in 1972 by S. P. Pavlou (personal communication) PCB levels averaging about 2300 ppb (dry wt) were found at the river mouth. The levels decreased gradually as the sediment samples were collected further upstream. Concentrations of PCB were about 500 ppb in areas where most fin erosion fish were captured.

Although the presence of elevated PCB levels in the tissues and environment of a population of fish with a significant frequency of fin erosion is not proof of cause, PCB may represent a contributing factor. Additional analyses of PCB, DDT, and heavy metals in starry flounders and English sole from the Duwamish River are currently being performed, and the results will be reported in a later publication.

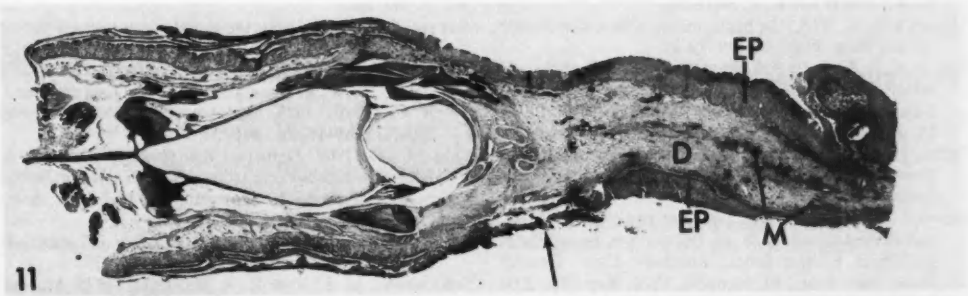
Mearns and Sherwood (1974) suspect that fin erosion in Dover sole from southern California coastal waters is the result of contact of fins with toxic bottom sediments. Since no evidence of a bacterial disease is found in eroded fin tissue of Dover sole and since compounds such as sulfides, metallic compounds, chlorinated hydrocarbons, acids, and alkalies are known to be in bottom sediments, the authors suggest that toxins may remove protective mucus from fins and expose the fin tissue to the necrosing action of agents in the sediment. More recently, Dover sole with fin erosion are reported to produce a much smaller amount of external mucus than normal-appearing Dover sole (Sherwood and Bendele 1975).

Recent observations (B. B. McCain and K. V. Pierce unpublished data) also show evidence of liver damage in fish collected in the Duwamish River in comparison to control fish collected in the lower reaches of another river where there is no fin erosion. Histological preparations of livers of starry flounder from the Duwamish River show increased fat deposition in hepatocytes, minimal fibrosis, and vascular distension. Further, the serum cholesterol of starry flounder and English sole from the Duwamish River averages 5.5 mg/ml, whereas, the value for the control fish is 1.4 mg/ml. Studies to determine whether this defect is incidental or intrinsic to the etiology and pathogenesis of fin erosion disease are being pursued.

As in other disease processes in any species, the observations best fit a multifactorial hypothesis of etiology, i.e. it is logical to assume that multiple environmental variables (such as chemical pollutants, physical factors, mechanical injury, etc.) act in some combination on a susceptible genetic background to produce a particular incidence of disease in the population at risk.

FIGURES 11–14

FIG. 11. Fin erosion showing epidermis (EP) that is hyperplastic, dermal fibrosis (D) with absence of fin rays, irregular distribution of melanophores (M), and focal ulceration of epidermis (arrow). H&E; 17×. FIG. 12. Chronic fibrosing fin erosion showing a longitudinal section of a fin ray. The two long spicules of the fin ray are intact at 1 and completely resorbed and replaced by fibrosis at 2. In this possible early lesion fin ray resorption has occurred without some of the changes (epidermal hyperplasia, marked dermal fibrosis, soft tissue folding) characteristic of more advanced lesions. H&E; 64×. FIG. 13. Cross section of fin ray. Spicule on right is intact, that on left almost completely resorbed. Note layer of basophilic cells along surface of resorbed ray (arrow). There is focal ulceration of epidermis (double arrows). H&E; 128×. FIG. 14. Section of fin cut longitudinally to fin rays. Irregular resorption of fin ray and collapse and folding of the soft tissue has produced shortening (retraction) and marked distortion. This is a section of a flap of folded fin like that seen grossly in Fig. 3. Scar tissue consisting of melanophores, collagen, and fibroblasts join the folded fin ray to proximal fin (arrow). H&E; 30×.



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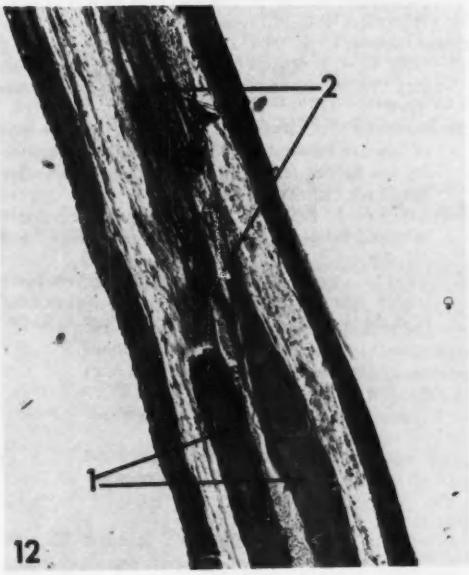

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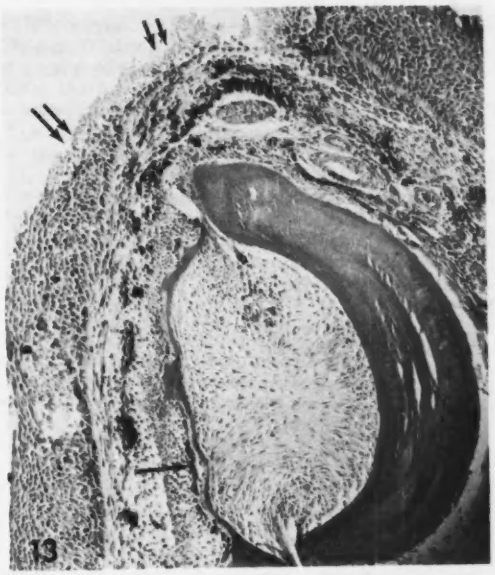

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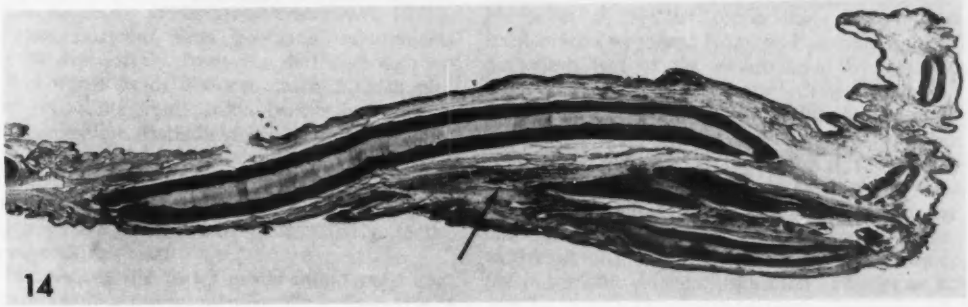

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Mineral Metabolism During the Ontogenesis of Rainbow Trout (*Salmo gairdneri*)[1]

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ZEITOUN, I. H., D. E. ULLREY, W. G. BERGEN, AND W. T. MAGEE. 1976. Mineral metabolism during the ontogenesis of rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 33: 2587–2591.

Rainbow trout (*Salmo gairdneri*) eggs were collected from three females, fertilized by the milt of two males per female, and incubated separately. Samples were taken before fertilization, at +0.5 h and on days 1, 1.5, 3, 4, 5, 13, 17, 21, at hatching (23 days), and on day 37, immediately after postyolk absorption. The water environment contributed an estimated minimum 26% of the Na, 30% of the Fe, and 13% of the Zn found at hatching. Derivation of Ca, Na, K, Fe, and Zn from the water environment at postyolk absorption was estimated to be at least 70, 76, 45, 68, and 2%, respectively. All the P and Cu at hatching and in the larva could have been derived from the unfertilized oocyte.

ZEITOUN, I. H., D. E. ULLREY, W. G. BERGEN, AND W. T. MAGEE. 1976. Mineral metabolism during the ontogenesis of rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 33: 2587–2591.

Des œufs de truite arc-en-ciel (*Salmo gairdneri*) ont été recueillis de trois femelles, fécondés par la laitance de deux mâles pour chaque femelle et incubés séparément. Des échantillons ont été prélevés avant la fécondation, à +0.5 h et aux jours 1, 1.5, 3, 4, 5, 13, 17, 21, à l'éclosion (23 jours) et au jour 37, immédiatement après résorption du vitellus. Le milieu aquatique a un minimum estimé de 26% du Na, 30% du Fe et 13% du Zn observés à l'éclosion. On estime que le Ca, Na, K, Fe et Zn dérivés du milieu aquatique au moment de la résorption du vitellus est d'au moins 70, 76, 45, 68 et 2% respectivement. Tout le P et le Cu présents au moment de l'éclosion et dans la larve ont pu provenir de l'ovocyte non fécondé.

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OVER 20 mineral elements have been shown to fulfill significant structural or metabolic functions in the tissues of vertebrates (Underwood 1971). In mammals and birds, postnatal requirements are derived largely from the diet, although ingested water (and, in some cases, inhaled air) may contribute significantly. During ontogenesis, the mammalian placenta serves as a nutrient conduit through which certain mineral elements are delivered from the maternal circulation to that of the embryo or fetus. In birds, the nutrients in the egg are transferred, nearly quantitatively, to the embryonating chick.

In teleosts, the water environment may contribute significantly to the mineral requirements of the adult and the young. Minerals may be absorbed and become a part of the tissues, or they may serve important functions in osmoregulation. Hayes et al. (1946) found that calcium and sodium were absorbed from, and phosphorus and potassium lost to the environment by eggs of Atlantic salmon (*Salmo salar*). The amount of ion movement is undoubtedly influenced by ionic concentration in the water. Phillips et al. (1962a) found that the eggs of brown trout (*S. trutta*) absorbed more calcium from hard water than from soft water. Furthermore, in fingerlings the calcium absorption mechanism seemed to be selective in that strontium additions to the water did not inhibit calcium absorption (Phillips et al. 1962b). Some translocation from the water environment to eggs and fry was also reported in rainbow trout (*S. gairdneri*) by Ogino and Yasuda (1962).

The objectives of this study were to trace the quantitative changes in mineral concentration from the unfertilized rainbow trout oocyte

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Table 1 - Ontogenetic stage of rainbow trout, dry weight per ontogenetic unit, and mineral concentration (dry basis). ^{a,b,c,d} means with different superscripts under the same heading are significantly different. ^{e}Standard error of the mean = $\sqrt{\frac{MSE}{n}}$; n = 3.

Description	Incubation day	Dry weight mg/Ou	Ca mg/g	P mg/g	Mg mg/g	Na mg/g	K mg/g	Fe ug/g	Cu ug/g	Zn ug/g
Unfertilized oocyte	0	42.1^{a}	0.9^{a}	10.9^{a}	1.4^{ab}	3.4^{a}	4.5^{a}	76.1^{ab}	13.1^{a}	61.7^{a}
Post-fertilized	(1/2 hr.)	40.7^{a}	0.9^{a}	10.7^{a}	1.5^{abc}	1.6^{b}	4.5^{a}	41.3^{a}	15.0^{a}	80.0^{ab}
Early cleavage	1	41.4^{a}	1.0^{a}	11.2^{ab}	1.5^{abc}	1.5^{b}	3.8^{a}	52.1^{ab}	13.1^{a}	66.3^{ab}
Early cleavage	1 1/2	42.2^{a}	1.1^{a}	11.9^{ab}	1.6^{bc}	1.3^{b}	3.3^{a}	36.4^{a}	14.4^{a}	73.6^{ab}
Early cleavage	3	41.6^{a}	1.1^{a}	10.5^{a}	1.4^{ab}	1.3^{b}	3.9^{a}	46.9^{ab}	20.2^{ab}	73.3^{ab}
Early blastula	4	41.2^{a}	0.9^{a}	10.7^{a}	1.5^{abc}	1.0^{b}	3.9^{a}	49.2^{ab}	54.0^{c}	74.4^{ab}
Late blastula	5	41.0^{a}	1.0^{a}	11.3^{ab}	1.6^{bc}	0.9^{b}	3.5^{a}	88.6^{b}	29.8^{b}	88.2^{ab}
Eyed stage	13	42.3^{a}	1.0^{a}	10.2^{a}	1.4^{ab}	0.9^{b}	3.3^{a}	34.7^{a}	43.9^{c}	71.8^{ab}
Organogenesis	17	41.4^{a}	1.1^{a}	10.7^{a}	1.4^{ab}	1.0^{b}	3.6^{a}	98.8^{b}	43.4^{c}	87.7^{ab}
Organogenesis	21	38.4^{ab}	1.0^{a}	10.1^{a}	1.3^{a}	1.2^{b}	3.9^{a}	54.4^{ab}	41.9^{bc}	76.2^{ab}
Hatched (fry + Yolk)	23	31.1^{bc}	1.1^{a}	11.9^{ab}	1.5^{abc}	1.7^{b}	3.7^{a}	70.6^{ab}	7.8^{a}	98.8^{ab}
Fry only	23	8.4^{d}	1.3^{a}	10.4^{a}	1.6^{bc}	1.4^{b}	3.9^{a}	70.9^{ab}	9.9^{a}	85.3^{ab}
Larva (post-yolk absorption)	37	25.0^{c}	4.7^{b}	12.3^{b}	1.7^{c}	6.1^{c}	8.3^{b}	183.1^{c}	8.9^{a}	105.9^{b}
SEM^{e}		2.38	0.09	0.41	0.06	0.25	0.35	7.90	2.65	8.14
Significance (P)		<0.01	<0.01	<0.05	<0.05	<0.01	< 0.01	<0.01	< 0.01	<0.05

through ontogenesis to hatching and postyolk absorption and to estimate the mineral contribution of the water environment to the developing embryo and the larva.

Materials and methods — Eggs were obtained from rainbow trout (*S. gairdneri*) caught at the Little Manistee River Weir, Manistee County, Michigan. Three groups of eggs were collected, each representing the eggs from one female. A sample of each group was frozen on dry ice, and the remaining eggs in each group were fertilized by the milt of two males and then water-hardened. One-half hour later a second sample from each group was frozen on dry ice.

The remaining fertilized eggs were incubated in flowing filtered well water with a temperature of 10–16 C and the following elemental concentrations ($SE = \sqrt{\frac{MSE}{n}}$; $n = 3$):

	mg/liter	SE
Ca	83.9	0.33
P	1.14	0.09
Mg	24.3	0.25
Na	5.7	0.41
K	1.2	0.01
Fe	0.28	0.01
Cu	0.01	0.0004
Zn	0.04	0.002

Additional samples were taken from each group daily for the first 5 days, followed by one sample every 2 days through the 2nd wk. During the remainder of incubation, one sample was taken weekly. After hatching, the larvae were kept in the incubator until the yolk was completely absorbed. At this time the final sample was obtained. (Most eggs hatched on the 23rd day of incubation, and complete absorption of the yolk took place 2 wk later.) All samples were stored at −20 C until analyzed.

The number of eggs per sample was counted, and dry matter concentrations were determined on each sample by drying a portion in a vacuum of 740 mm at 65 C for 18 h.

For mineral analyses, wet eggs, fry, or larvae were homogenized with deionized, distilled water. The homogenates were wet ashed using 60 ml of concentrated nitric acid followed by 7 ml of perchloric acid. Standards were processed in the same manner. Concentrations of calcium, magnesium, iron, copper, and zinc were determined by atomic absorption, sodium and potassium by atomic emission, and phosphorus by the method of Gomori (1942) using visible light spectrophotometry.

Data were tested for significance by analysis of variance. Comparisons between means were made using the Tukey test (Snedecor 1956). Since the ontogenetic stages were sequential, a bias was introduced into Tukey's test, but this test gives an approximation of the significance of the differences among the means.

Results — The average weights per ontogenetic unit (one egg or the developmental stage originating from one egg) at each developmental stage are presented in Table 1. Most eggs hatched on day 23 of incubation, and yolk absorption was complete on day 37. The term fry has been used for the newly hatched embryo minus yolk. The term larva has been used for the immediate postyolk absorption stage.

Significant ($P < 0.05$ or $P < 0.01$) effects of developmental stage on concentration were noted for each element assayed (Table 1). Fertilization and water hardening resulted in relatively large declines in sodium and iron, as compared with the unfertilized oocyte. During the remainder of incubation, iron and copper concentrations varied most widely.

Elemental concentrations per ontogenetic unit (OU) are presented in Fig. 1, from which estimates were made of the relative contributions of

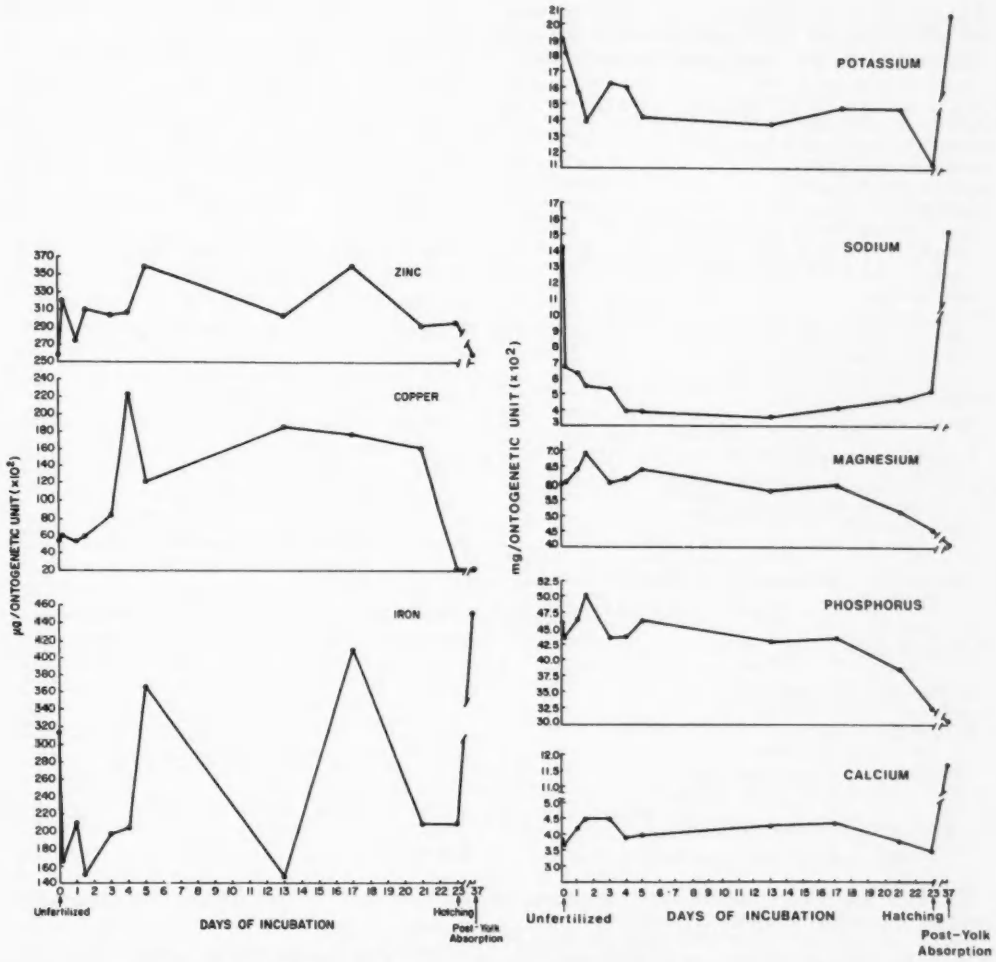

FIG. 1. Changes of calcium, phosphorus, magnesium, sodium, potassium, iron, copper, and zinc concentration at various stages of rainbow trout (*Salmo gairdneri*) ontogenesis.

the unfertilized oocyte and the water environment to mineral content of the newly hatched fry and yolk (Table 2) and the larva at postyolk absorption. The estimates of contributions of the unfertilized oocyte and the yolk represent maximum values since minerals, originally a part of these tissues, may not be quantitatively incorporated into the fry plus yolk or larva, and significant but undefined losses into the environment may occur. For the same reasons, estimates of the contribution of the water environment to the fry plus yolk or larva are minimum values.

If one compares the elemental concentration per ontogenetic unit in the unfertilized oocyte with that in the fry plus yolk, one might conclude that the mineral content of the former could account for the entire mineral content of the latter, except for zinc. However, during ontogenesis and before hatching, the sodium and iron concentration per ontogenetic unit fell below that in the unfertilized oocyte. Therefore, the unfertilized oocyte could not be expected to furnish more than these minimum values. Those estimates derived from a developmental stage that is intermediate between the unfertilized oocyte and the yolk plus fry at hatching are shown in paren-

TABLE 2. Relative contributions of the unfertilized oocyte and the water environment to mineral content of the newly hatched fry plus yolk and the larva at postyolk absorption.

	Ca	P	Mg	Na	K	Fe	Cu	Zn
Amount in unfertilized oocyte (μg/OU)[a]	37.7	455.7	59.5	142.1	191.2	3.18	0.55	2.58
Amount in fry plus yolk (μg/OU)	35.4	354.2	46.2	51.4	114.7	2.10	0.24	2.97
Amount in fry (μg/OU)	10.5	84.9	12.9	11.0	32.3	0.58	0.08	0.71
Amount in yolk (μg/OU)	24.9	269.3	33.3	40.4	82.4	1.52	0.16	2.26
Amount in larva (μg/OU)	116.7	306.9	41.2	152.2	207.8	4.57	0.22	2.64
Proportion (max) in fry plus yolk derived from oocyte (%)[b]	100	100	100	(74.1)[i]	100	(69.9)	100	86.9
Proportion (min) in fry plus yolk derived from water (%)[c]	—	—	—	(25.9)	—	(30.1)	—	13.1
Proportion (max) in larva derived from oocyte (%)[d]	(29.6)	100	100	(23.7)	(55.2)	(32.5)	100	97.7
Proportion (min) in larva derived from water (%)[e]	(70.4)	—	—	(76.3)	(44.8)	(67.5)	—	2.3
Proportion (max) in larva derived from fry (%)[f]	9.0	27.7	31.3	7.2	15.5	12.7	36.4	26.9
Proportion (max) in larva derived from yolk (%)[g]	21.3	87.8	80.8	26.5	39.7	33.3	72.7	85.6
Proportion (min) in larva derived from water between hatching and yolk absorption (%)[h]	69.7	—	—	66.3	44.8	54.0	—	—

[a] Ontogenetic unit (one egg or the developmental stage originating from one egg).

[b] $\frac{X_o}{X_{f+y}} \times 100$; X_o = amount in unfertilized oocyte; X_{f+y} = amount in fry plus yolk.

[c] $\frac{(X_{f+y}) - X_o}{X_{f+y}} \times 100$.

[d] $\frac{X_o}{X_l} \times 100$; X_l = amount in larva.

[e] $\frac{X_l - X_o}{X_l} \times 100$.

[f] $\frac{X_f}{X_l} \times 100$; X_f = amount in fry.

[g] $\frac{X_y}{X_l} \times 100$; X_y = amount in yolk.

[h] $\frac{X_l - (X_{f+y})}{X_l}$

[i] Values in parentheses calculated from a developmental stage intermediate between the unfertilized oocyte and hatching or postyolk absorption.

theses. Similar adjustments were necessary in calculating the contribution of the unfertilized oocyte to the larva. Taking these calculations into account, at least 26% of the sodium, 30% of the iron, and 13% of the zinc in the fry plus yolk at hatching were derived from the water environment. From hatching to postyolk absorption, at least 70% of the calcium, 66% of the sodium, 45% of the potassium, and 54% of the iron were derived from the water environment. Over the entire study period, at least 70% of the calcium, 76% of the sodium, 45% of the potassium, 68% of the iron, and 2% of the zinc in the larva were derived from the water environment.

Discussion — Knight (1963) has described the morphology of embryonic and larval development of rainbow trout, and an attempt has been made to relate the changes in mineral concentration noted in this study to these morphological events.

The decline in sodium concentration from the unfertilized oocyte to postfertilization at ½ hour may have been associated with removal of sodium in fluids washed away from the oocyte surface during hardening in water or with the movement of sodium out of the oocyte into the hypotonic water medium. Kalman (1959) has provided evidence for water exchange between yolk sac and medium in the water-hardened unfertilized egg. It is reasonable to expect some ion exchange associated with this movement of water. There was also a rather large decline in iron concentration during this period but the decline was not statistically significant.

The other major concentration changes during

prehatching ontogenesis involved iron and copper. At 1½ days, when the cells of the blastoderm were becoming smaller and more numerous, iron concentration reached a low point. By 5 days, when 17–24 somites are visible, the iron concentration reached a peak. During the next 8 days, additional somites develop and the mesenchymal cells form blood constituents in the areas of the yolk sac adjacent to the body of the embryo. The heart migrates from anterior to the head to a new position ventral to the gill buds. Erythrocytes are circulating through the blood vessels at 11 days, and by 13 days the gills are prominent and iron concentration has reached a second low point. Most of the development from this point on involves an increase in size. Iron concentration reached a second peak at 17 days, followed by a marked decline at 2 days before hatching. The large increase in iron concentration from hatching to postyolk absorption may be associated with the transition in erythrocytes from the larval to the adult type (Iuchi 1973).

Copper concentration gradually increased from 1 to 13 days except for a remarkable peak at 4 days, when the endoderm appears under the embryonic shield. At the time of hatching, copper levels dropped precipitously, possibly coincident with separation of the shell (although the shells were not analyzed separately for their copper content).

Zinc concentrations reported in the roe of carp (*Cyprinus carpio*) by Sabodash (1970) were much higher than we observed in rainbow trout. Wedemeyer (1968) found a significant uptake of ^{65}Zn by coho salmon (*Oncorhynchus kisutch*) eggs during incubation, but a net zinc accumulation was not apparent in rainbow trout eggs during ontogenesis in our study.

These data establish that the dynamic exchange of minerals between teleost eggs and the water medium, in which ontogenesis occurs, contributes meaningfully to the ultimate elemental concentration of rainbow trout larva. Quantitative measurement of net effects indicates that the water medium may contribute significant amounts of calcium, sodium, potassium, and iron. As a consequence, it is important to know (and may be important to control) the mineral concentration of the water in which teleost eggs are incubated.

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Relation of Number of Eggs and Egg Length to Carapace Width in the Brachyuran Crabs *Chionoecetes bairdi* and *C. opilio* from the Southeastern Bering Sea and *C. opilio* from the Gulf of St. Lawrence

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HAYNES, E., J. F. KARINEN, J. WATSON, AND D. J. HOPSON. 1976. Relation of number of eggs and egg length to carapace width in the brachyuran crabs *Chionoecetes bairdi* and *C. opilio* from the southeastern Bering Sea and *C. opilio* from the Gulf of St. Lawrence. J. Fish. Res. Board Can. 33: 2592–2595.

The number of eggs attached to pleopods of *Chionoecetes bairdi* and *C. opilio* from the southeastern Bering Sea increased at a rate proportional to about the 3.4 and 2.7 power of carapace width, respectively, but for *C. opilio* from the Gulf of St. Lawrence it increased to the 4.2 power. The range in carapace width and number of eggs for crabs from the Bering Sea of a given carapace width were considerably greater for *C. bairdi* than for *C. opilio*. In the southeastern Bering Sea, the reproductive potential for adult females of *C. bairdi* with mixed spawning history is approximately 4 times greater than that of *C. opilio* spawning for the first time. *Chionoecetes opilio* females with mixed spawning history in the Gulf of St. Lawrence carry more eggs for a given carapace width than first-time spawners from the southeastern Bering Sea. Our data were not sufficient to resolve the question of relative number of eggs for crabs of various ages.

HAYNES, E., J. F. KARINEN, J. WATSON, AND D. J. HOPSON. 1976. Relation of number of eggs and egg length to carapace width in the brachyuran crabs *Chionoecetes bairdi* and *C. opilio* from the southeastern Bering Sea and *C. opilio* from the Gulf of St. Lawrence. J. Fish. Res. Board Can. 33: 2592–2595.

Chez *Chionoecetes bairdi* et *C. opilio* du sud-est de la mer de Béring, le nombre d'œufs fixés aux pléopodes augmente à un rythme proportionnel aux puissances d'environ 3.4 et 2.7, respectivement, à la largeur de carapace, mais chez *C. opilio* du golfe Saint-Laurent, il augmente à la puissance de 4.2. Pour des crabes de la mer de Béring d'une largeur de carapace donnée, la gamme de largeur de carapace et de nombre d'œufs est beaucoup plus étendue chez *C. bairdi* que chez *C. opilio*. Dans le sud-est de la mer de Béring, le potentiel reproducteur des femelles adultes de *C. bairdi* à passé de ponte mixte est approximativement 4 fois plus grand que celui de *C. opilio* pondant pour la première fois. Les femelles de *C. opilio* à passé reproducteur mixte dans le golfe Saint-Laurent portent plus d'œufs, pour une largeur de carapace donnée, que celles qui pondent pour la première fois dans le sud-est de la mer de Béring. Nos données ne nous permettent pas de résoudre la question du nombre relatif d'œufs chez des crabes de divers âges.

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Two species of brachyuran crabs (subfamily Majidae) *Chionoecetes bairdi* and *C. opilio* (commonly called tanner or snow crabs) are fished commercially in the eastern Pacific Ocean. *Chionoecetes opilio* is also fished commercially in the Gulf of St. Lawrence. Because estimates of fecundity are useful for studying the population dynamics of a stock, especially the effects of a high exploitation rate on reproductive potential, the present study was undertaken to determine

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the number of eggs attached to the pleopods of *C. bairdi* and *C. opilio*. In this note we describe the relation of number of eggs attached to the pleopods and egg diameter to carapace width for *C. bairdi* and *C. opilio* from the southeastern Bering Sea and for *C. opilio* from the Gulf of St. Lawrence. We also estimate the relative reproductive potential of the two species from the southeastern Bering Sea.

Sample collection and treatment — Egg samples were collected from crabs from the southeastern Bering Sea and the Gulf of St. Lawrence. The 42 *C. bairdi* and 23 *C. opilio* samples from the Bering Sea were collected incidentally during a trawl survey by the National Marine Fisheries Service from September 19 to October 3, 1969 (Fig. 1). Other objectives took precedence over this study, hence the small sample size taken. The 99 Gulf of St. Lawrence samples were from *C. opilio* caught in traps in May and June 1968 at two locations off the Gaspé Peninsula. The traps were set approximately 400 m apart extending for 3.2 km and ranging from 72 to 144 m deep. The trap locations were at 48°43′30″N, 64°10′00″E near Gaspé Bay and 48°21′00″N, 64°21′20″E near Chaleur Bay.

In both the Bering Sea and Gulf of St. Lawrence, crabs were arbitrarily selected to ensure representation of all sizes of ovigerous females. All ovigerous *C. opilio* from the Bering Sea were from first-time spawners, whereas ovigerous *C. bairdi* from the Bering Sea and *C. opilio* from the Gulf of St. Lawrence included crabs with mixed spawning history, i.e. first-, second-, and third-time spawners. The spawning history of each crab was estimated according to external wear and appearance of the exoskeleton (shell condition) using the procedure reported by Watson (1969). Eggs from crabs from both the Gulf of St. Lawrence and the Bering Sea were in the early stages of development when sampled.

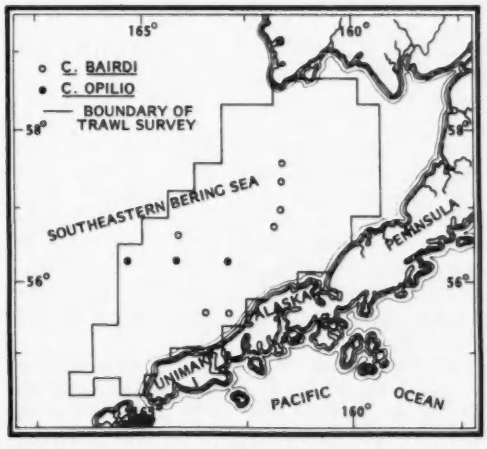

FIG. 1. Southeastern Bering Sea showing locations where *Chionoecetes bairdi* and *C. opilio* were collected to determine number of eggs–carapace width relation.

Procedures for estimating number of eggs attached to pleopods and egg diameter were identical for all crabs. Crabs were selected from the trawl and trap catches and measured to the nearest millimeter across their greatest carapace width, excluding spines. The egg mass, with pleopods attached, was then removed by excising the pleopods at their bases. Individual egg masses were preserved in 10% formalin in jars and identified by carapace width of specimen, spawning history, date, and location of capture.

Eggs from each mass were separated from the pleopods, blotted, and weighed to an accuracy of ±0.01 g. About 5% of the eggs were randomly removed, weighed, and counted. For counting, the eggs were first dried for several days at room temperature and then gently rubbed to free them from connective tissue. Repeated counts of several samples gave a maximum counting error of 0.3%. The number of eggs was determined by weighing the total egg mass and a representative sample, counting the eggs in the sample, and calculating the total number of eggs by dividing the total weight by the sample weight and multiplying the resulting quotient by the number of eggs in the sample.

To determine egg diameter, a sample of eggs was randomly removed from the blotted egg mass, and the lengths of 25 of the eggs were measured to 0.01 mm with the aid of an ocular micrometer.

Relation between number of eggs and carapace width — Because we considered the data to be nonrandom but symmetrical samples from a hypothetical distribution of observations of uniform density and of indefinite extent, we used the geometric mean regression as defined by Ricker (1973) as the appropriate measure of the functional regression of Y on X. Ricker's notations are followed and are equivalent to notations in the allometric equation as follows: $X = W$, $u = a$, and $v = B$.

To estimate the parameters of the allometric equation, we applied a logarithmic transformation ($\log_e$) to the two variables, and the relationship between log fecundity and log width was expressed in the form:

$$\log_e Y = \log_e u + v \log_e X$$

The correlation coefficients are high for both species (Table 1), indicating a real relationship between number of eggs and carapace width.

We used 95% confidence intervals of the regression coefficients (v) to provide information on the null hypothesis that the slope equalled 3 for each species in both areas (Table 1). The regression coefficients for *C. bairdi* (Fig. 2) and *C. opilio* (Fig. 3) from the Bering Sea are not

TABLE 1. Relationship of $\log_e$ number of eggs to $\log_e$ carapace width for *Chionoecetes opilio* from the southeastern Bering Sea and Gulf of St. Lawrence and *C. bairdi* from the southeastern Bering Sea.

Species and area	n	Regression coefficient v	95% confidence limits	Intercept $\log_e$ (u)	Correlation coefficient (v)
		Chionoecetes opilio			
Southeastern Bering Sea	23	2.7206	±0.7265	−0.7124	0.8086
Gulf of St. Lawrence	99	4.2000	±0.5686	−6.7472	0.7329
		C. bairdi			
Southeastern Bering Sea	42	3.3754	±0.7135	−3.2586	0.7313

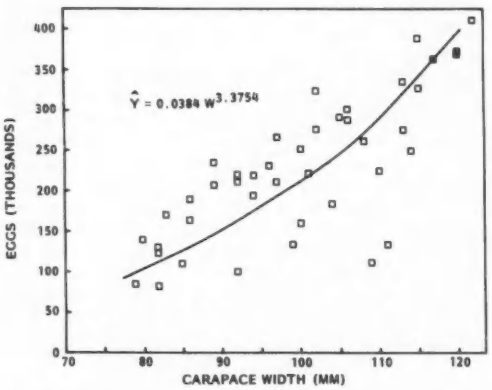

FIG. 2. Estimates of number of eggs of 42 *C. bairdi* collected in the southeastern Bering Sea in September–October 1969 and computed linear regression of number of eggs on carapace width.

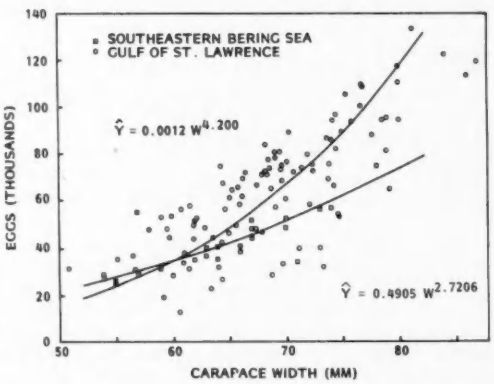

FIG. 3. Estimates of number of eggs of 99 *C. opilio* collected in the Gulf of St. Lawrence in 1968 and 23 collected in the southeastern Bering Sea in September–October 1969 and computed linear regressions of number of eggs on carapace width.

significantly greater than 3, but the regression coefficient for *C. opilio* from the Gulf of St. Lawrence is significantly greater than 3. Apparently, for *C. opilio* from the Gulf of St. Lawrence, number of eggs increases at a rate greater than width of crab (Fig. 3).

The observed range in number of eggs for a given carapace width is greater for *C. opilio* from the Gulf of St. Lawrence than for *C. opilio* from the southeastern Bering Sea (Fig. 3). Maximum difference between lowest and highest number of eggs in a 5-mm size-group for *C. opilio* in the southeastern Bering Sea was 30,452 eggs (55–59 mm) and the mean difference was 17,857 eggs. For *C. opilio* in the Gulf of St. Lawrence, maximum difference was 64,787 eggs (70–74 mm) and the mean difference was 52,088 eggs.

Cause of differences in number of eggs between species and areas — The difference in number of eggs carried by adult *C. bairdi* females from the Bering Sea with mixed spawning history and adult *C. opilio* from the Gulf of St. Lawrence with similar spawning history may be related to differences in the relative size of crabs and eggs for these two species. *Chionoecetes bairdi* are larger and have smaller eggs and therefore can carry a greater number of eggs. However, *C. bairdi* from the Bering Sea and *C. opilio* from the Gulf of St. Lawrence of similar size (80-mm carapace width) appear to carry approximately the same number of eggs (Fig. 2 and 3). Therefore, at this size, at least, other factors apparently control the number of eggs extruded.

An explanation for the differences in numbers of eggs carried by *C. opilio* females from the Bering Sea and the Gulf of St. Lawrence is not so clear. In this study, an obvious difference between two groups was spawning history. The *C. bairdi* from the southeastern Bering Sea and *C. opilio* from the Gulf of St. Lawrence used as sources of eggs ranged from first-time spawners

to females that had probably produced at least three annual egg clutches. In contrast, the *C. opilio* from the southeastern Bering Sea were all first-time spawners. Unfortunately, differences in success of egg attachment between first- and second- or third-time spawners are not known and data are not sufficient to resolve the question.

Egg size — For Bering Sea samples, individual maximum diameters of preserved eggs ranged from 0.49 to 0.66 mm (grand mean 0.56 mm) for *C. bairdi*, and from 0.56 to 0.74 mm (grand mean 0.66 mm) for *C. opilio*. Egg size was uniform in the Bering Sea samples; coefficients of variation ranged from 1.4 to 6.0% for *C. bairdi* and from 1.1 to 5.4% for *C. opilio*. Similarly, egg size was uniform among the Gulf of St. Lawrence samples (range 0.56–0.75 mm; grand mean 0.65 mm). No significant correlation was found between mean egg size and crab size for crabs from either the Bering Sea ($r = 0.232$, $n = 23$ for *C. opilio*; $r = 0.246$, $n = 42$ for *C. bairdi*) or Gulf of St. Lawrence ($r = 0.071$, $n = 99$ for *C. opilio*).

Reproductive potential — Comparison of the number of eggs and carapace width for *C. bairdi* and *C. opilio* (Fig. 2 and 3) in the southeastern Bering Sea shows that adult females of *C. bairdi* of mixed spawning history have a higher reproductive potential than first-time spawners of *C. opilio*. This potential can be assessed by comparing estimates of the calculated number of eggs for both species. The estimates were computed using the midpoints of the 5-mm width class intervals and include the major portion of the size range of all ovigerous *Chionoecetes* caught during the trawling survey. Comparison of the calculated numbers of eggs for both species shows that for an equivalent number of spawners, the reproductive potential of adult females of *C. bairdi* with mixed spawning history is approximately 4 times greater than that of 1st-yr spawning *C. opilio* (Table 2). The average number of eggs per female for the 1,854 ovigerous *C. opilio* captured during the survey was calculated to be 36,273 eggs, and the average for the 2,817 ovigerous *C. bairdi* was 150,912 eggs. It is not known whether this relationship will hold when second- and third-time spawning *C. opilio* are compared with *C. bairdi* with a similar spawning history.

TABLE 2. Mean and weighted number of eggs for *C. opilio* and *C. bairdi* captured on trawl survey in southeastern Bering Sea, September 19–October 3, 1969.

	C. opilio	*C. bairdi*
No. ovigerous crabs captured	1,854	2,817
Mean no. eggs ($\times 10^3$)	36,273	150,912
Weighted no. eggs for all crabs ($\times 10^5$)	673	4,251

If the reproductive potential of *C. bairdi* remains about 4 times that of *C. opilio* regardless of spawning age, estimates of the reproductive potential of the stocks of *C. bairdi* and *C. opilio* within the trawl survey area can be determined by comparing the weighted number of eggs derived from the width frequencies and relative abundance of each species. Comparison of the weighted numbers of eggs shows that within the trawl survey area in 1969, the reproductive potential for the stock of *C. bairdi* was approximately 6 times greater than for the stock of *C. opilio*. However, the trawl survey did not include all areas in the southeastern Bering Sea inhabited by *Chionoecetes*. Karinen (1974) found that ovigerous *C. bairdi* and *C. opilio* occur westward of the trawl survey area to at least the Pribilof Islands. It is not known whether the reproductive potential ratio of about 6:1 holds throughout all areas when the two species occur together.

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Method of Counting Tailbeats of Free-Swimming Fish by Ultrasonic Telemetry Techniques

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STASKO, A. B., AND R. M. HORRALL. 1976. Method of counting tailbeats of free-swimming fish by ultrasonic telemetry techniques. J. Fish. Res. Board Can. 33: 2596–2598.

Rhythmic beats in ultrasonic signals from free-swimming fish fitted with continuous-wave transmitters were noted during tracking of four species. Such signal beats corresponded with visually observed tailbeats of salmon and are presumed to have resulted from a Doppler effect due to undulations of the body and tail. The beats cannot be detected from pulsed transmitters. Tailbeat frequencies of white bass (*Morone chrysops*) were higher than those of salmon for the same swimming speed in body lengths per second.

STASKO, A. B., AND R. M. HORRALL. 1976. Method of counting tailbeats of free-swimming fish by ultrasonic telemetry techniques. J. Fish. Res. Board Can. 33: 2596–2598.

Au cours du dépistage de quatre espèces, nous avons observé des battements rythmiques dans les signaux ultrasonores reçus de poissons nageant librement et sur lesquels étaient fixés des émetteurs à ondes continues. De tels signaux correspondent aux battements de queue observés visuellement chez le saumon, et on suppose qu'ils résultent d'un effet Doppler causé par les ondulations du corps et de la queue. Ces battements ne peuvent pas être détectés quand des émetteurs pulsés sont utilisés. La fréquence des battements de queue du bar-perche (*Morone chrysops*) est plus grande que ceux du saumon à une même vitesse de nage en longueurs de corps par seconde.

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IN some of our early biotelemetry studies on orientation and migration of fishes we used continuous-wave ultrasonic transmitters (Hasler et al. 1969; McCleave and Horrall 1970; Stasko et al. 1973, 1976). While tracking white bass (*Morone chrysops*), cutthroat trout (*Salmo clarki*), pink (*Oncorhynchus gorbuscha*), and sockeye (*O. nerka*) salmon fitted with such transmitters, we frequently noted rhythmic beats in the signals.

In this note we present evidence directly relating signal beats to tailbeats of fish. These observations show that continuous-wave (as opposed to pulsed) ultrasonic transmitters can be used to count tailbeats of free-swimming fish.

Observations and analysis — The beat in signals from fish-borne continuous-wave transmitters is a change in quality of the audio signal from an HRO 500 receiver (National Radio Co., Melrose, Massachusetts). Such a change in tone can be simulated by back-and-forth movement of the frequency-adjust knob in the presence of an unchanging incoming signal. We interpreted the beat to be a change in carrier frequency of the signal from the fish-borne transmitters.

During most of the tracking studies the signal beats received little attention, but occasional comments, including some counts of beat frequency, were noted on the data sheets. With time, we came to associate the beats with periods of active swimming of the fish, although sometimes a moving fish would not produce a noticeable beat. Changing orientation of the body axis relative to the hydrophone may account for this.

To verify the source of the beats we placed a pink salmon fitted with a continuous-wave ultrasonic transmitter in a hoopnet alongside our 5-m boat. The net was towed at a slow speed such that the fish could swim without touching the net. A hydrophone facing the fish broadside at the opposite side of the boat was used for listening to the signal beats while a simultaneous visual count was made of tailbeats of the fish. Beats in the signal matched the visually observed tailbeats.

During tracking of white bass (Hasler et al.

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1969) 8 counts of signal beats/min were recorded for five free-swimming fish 30.1–32.7 cm long. The field notes contained numerous other references to such beats but with no recorded counts. Corresponding swimming speeds of the fish were determined from sextant readings with corrections made for water currents. Beats per minute at 15–20 C are plotted against observed swimming speed at the top of Fig. 1. The calculated regression line is $y = 98.5 + 74.7x$. The coefficient of correlation is 0.657; this is significant at the 10% level despite the considerable error inherent in short-term estimates of swimming speed.

More signal beats were obtained for adult pink salmon and sockeye salmon (Stasko et al. 1973, 1976). Altogether 110 counts for 22 fish, with an average body length (BL) of 63 cm (59–67 cm), ranged from 60 to 170 beats/min. Although simultaneous swimming speeds were not measured, tailbeats at these rates correspond to swimming speeds of approximately 0.4–1.7 BL/s; this is based on Brett's observations on 51–56-cm sockeye salmon swimming in a respirometer tunnel 17.8 cm diam (lower lines in Fig. 1, data from J. R. Brett personal communication). For our 63-cm fish the 0.4–1.7 lengths/s convert to speeds of 25–107 cm/s. These are well within the range of cruising speeds observed for the same fish (Stasko et al. 1973).

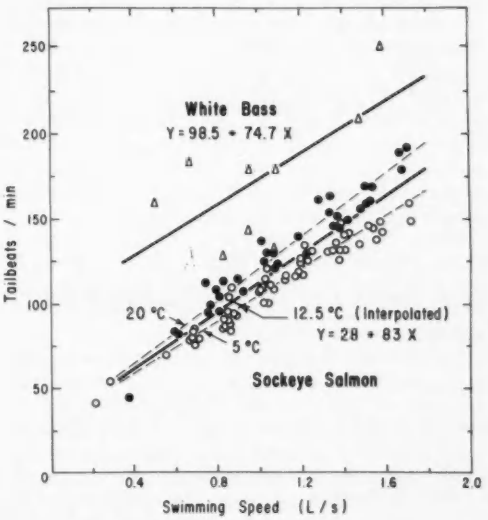

FIG. 1. Measurements of tailbeat frequency for 30–33-cm white bass (*Morone chrysops*) (△), are from sonic-tagged fish in an open lake. One tailbeat includes a full movement of the tail from right to left and back to right again. Measurements for 51–56-cm sockeye salmon (*Oncorhynchus nerka*) were done in a 17.8 cm diam respirometer tunnel (data from J. R. Brett personal communication); ○, for 5 C; ●, for 20 C.

Comparison of tailbeat frequencies of white bass and sockeye salmon for a given speed in body lengths per second (Fig. 1) shows a faster tailbeat for white bass. The white bass has a laterally compressed body compared to the more streamlined shape of salmonids.

Signal beats were also noted during tracking of cutthroat trout, but only two actual counts of 165 and 170 beats/min, without corresponding swimming speeds, were recorded for a single 40-cm fish (McCleave and Horrall 1970; and unpublished data).

Discussion — The relation between tailbeat frequency and swimming speed of fish has been studied under laboratory conditions in various tanks and forced-swimming apparatus, and under field conditions by visual observation, by continuous-transmission frequency modulated sonar, by sector-scanning sonar, and by ultrasonic telemetry techniques. Most studies have been in the laboratory (Bainbridge 1958; Hunter and Zweifel 1971; Magnuson and Prescott 1966), often associated with respiration physiology research (Roberts 1975; Shelton 1970).

Observations under natural conditions are few. Visual observations on yellowfin (*Thunnus albacares*) and skipjack tuna (*Euthynnus pelamis*) were made from an underwater observation chamber on a research vessel (Yuen 1966). Hester (1967) analyzed echo patterns from a continuous transmission FM sonar in an attempt to indentify some scombroids on the basis of Doppler effects from body and tail motions of the target fish. Harden Jones (1973) described the speed and tailbeats of one large shark observed for about 3 min by sector-scanning sonar. Young et al. (1972) described an ultrasonic transmitter with an external bimorph element designed to modulate the carrier frequency in response to instantaneous changes in swimming speed of a fish.

Our method of counting tailbeats depends on beats in continuous-wave signals originating from turbulence systems, set up by movements of the body and tail, presumably resulting in a Doppler effect. This is a simple method requiring no special equipment other than that used for ultrasonic tracking of fish. It can be used with a transmitter placed in the stomach or implanted into the body cavity.

In our studies the transmitter was in the gut of salmon and white bass, and attached behind the

dorsal fin of cutthroat trout. Beats in the signal were obtained from both locations. Carrier frequencies were 50 kHz for salmon, 65 kHz for white bass, and 30–75 kHz for cutthroat trout. Advantages of different carrier frequencies for enhancing the beat have not been investigated.

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Growth Inhibition Caused by Turbulence in the Toxic Marine Dinoflagellate *Gonyaulax excavata*

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WHITE, A. W. 1976. Growth inhibition caused by turbulence in the toxic marine dinoflagellate *Gonyaulax excavata*. J. Fish. Res. Board Can. 33: 2598–2602.

The effects of agitation on growth of *Gonyaulax excavata* were determined using laboratory cultures. Continuous rotary shaking of cultures at speeds of 125 rpm and greater caused rapid death and disintegration of cells, while shaking at slower speeds caused inhibition of growth rate compared to nonshaken cultures. Also, intermittent shaking, even for as little as 30 min/day, caused growth inhibition. The study suggests that small-scale, oceanic turbulence of sufficient intensity may inhibit growth of individual dinoflagellate cells.

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WHITE, A. W. 1976. Growth inhibition caused by turbulence in the toxic marine dinoflagellate *Gonyaulax excavata*. J. Fish. Res. Board Can. 33: 2598–2602.

Des cultures en laboratoire ont été utilisées pour mesurer les effets de l'agitation sur la croissance de *Goniaulax excavata*. L'agitation rotatoire continue des cultures à des vitesses de 125 rpm et plus entraîne une mort rapide et une désintégration cellulaire, alors que l'agitation à des vitesses moindres inhibe le rythme de croissance par comparaison avec des cultures non agitées. En outre, l'agitation intermittente, même durant une période aussi courte que 30 min/jour, inhibe la croissance. D'après cette étude, une turbulence océanique à petite échelle mais d'intensité suffisante pourrait inhiber la croissance de cellules individuelles de dinoflagellés.

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THE toxic dinoflagellate responsible for paralytic shellfish poisoning in eastern Canada and New England is *Gonyaulax excavata* (Braarud) Balech, as recently described by Loeblich and Loeblich (1975). This organism has been commonly referred to as *G. tamarensis*, which is a very closely related, but nontoxic species originally isolated from the Tamar River estuary in England.

Gonyaulax excavata occurs regularly in the summer plankton in the Bay of Fundy and sporadically in the St. Lawrence River estuary and the western Gulf of St. Lawrence (Prakash et al. 1971), necessitating the closure of shellfish beds. Recently, "red tides" of this organism have occurred along the New England coast (Hartwell 1975; Mulligan 1975). The reason for the distribution of *G. excavata* is not known, but may be related to the presence of land-derived organic substances in coastal waters (Prakash and Rashid 1968).

During studies of the growth of *G. excavata* in laboratory cultures, shaking of the cultures caused a marked depression in growth. Similar observations have been made on other marine dinoflagellates (Galleron 1976; Tuttle and Loeblich 1975). When combined with the observations that blooms of marine dinoflagellates generally appear during periods of calm weather and when the water column is relatively stable (Prakash et al. 1971; Ryther 1955; Wyatt 1975), it suggests that turbulence in nature may have direct effects on the physiology and growth of individual dinoflagellate cells, as well as on the spatial structure and distribution of entire populations.

This paper presents the results of studies on the effects of agitation on the growth of *G. excavata* in culture and discusses the possible significance of these results in terms of turbulence and dinoflagellate blooms in nature.

Materials and methods — The isolate of *G. excavata* used in this study was obtained from H. Stanley and D. Wall at the Woods Hole Oceanographic Institution, and was originally isolated by C. Martin from a bloom off Cape Ann, Massachusetts, during the summer of 1972. It is probably the same isolate as strain 429 used by Loeblich and Loeblich (1975) for their description of *G. excavata*, because strain 429 has the same history.

The enriched filtered-seawater medium "f" (Guillard and Ryther 1962) was used at half-strength, with the exception that silicate was not added. The medium was made using sea water from the Bay of Fundy with a salinity of 30–32‰, aged for several months in polyethylene carboys. Axenic cultures were grown in 50 ml of medium in cotton-stoppered, 125-ml Erlenmeyer flasks, autoclaved for 15 min at 121 C.

Both stock and experimental cultures were grown at 10–11 C and at a light intensity of 4000 lx from cool-white fluorescent lamps on a daily 14-h photoperiod. Under these conditions the generation time in standing cultures without forced aeration is about 3 days, and there may or may not be a lag period lasting up to 6 days. Inocula were always made with cells in late log phase growth, and initial cell densities were around 500 cells/ml. All experimental treatments were made in duplicate.

Cell numbers were determined using settling chambers or Palmer–Maloney chambers (0.1 ml capacity). Generally, at least a total of 400 cells were counted in two replicate fields. Counts were made every 3 days and cultures were thoroughly shaken by hand before sampling. Flasks were agitated using Model G-2, rotary shakers (New Brunswick Scientific) with a 1.9-cm circular orbit.

Results — *Gonyaulax excavata* was grown without shaking and with continuous rotary shaking at 100, 110, 125, 130, and 140 rpm. At shaking speeds of 125 rpm and greater, cells died rapidly and disintegrated. At 110 rpm and slower there was inhibition of growth compared to controls, and the inhibition depended upon the degree of agitation. Growth curves for nonshaken cultures and cultures shaken at 100 and 125 rpm are shown in Fig. 1. The generation times in the duplicate control flasks were 2.5 and 2.8 days, whereas they were 3.0 and 3.4 days at 100 rpm. At 110 rpm (curves not shown) the generation time was 4.9 days. The rapid death and disap-

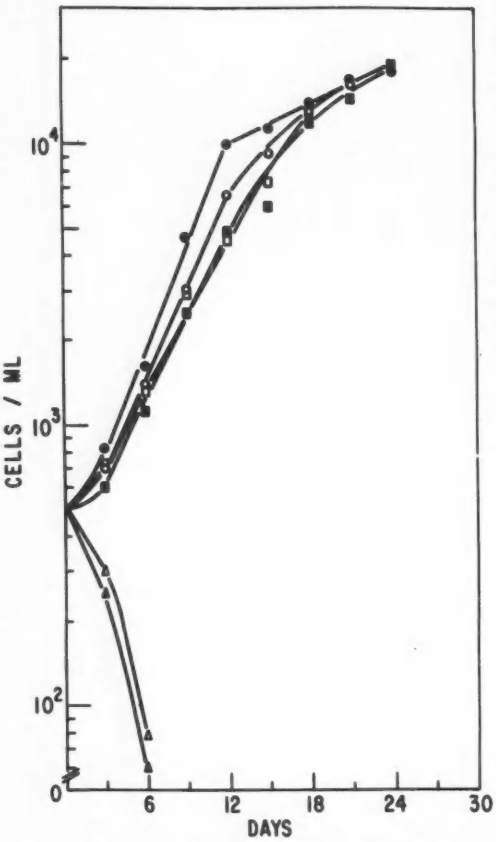

FIG. 1. Growth of *Gonyaulax excavata* without shaking (●, ○) and with continuous shaking at 100 rpm (■, □) and at 125 rpm (▲, △).

pearance of cells at 125 rpm is apparent from the figure; results at 130 and 140 rpm were the same.

During shaking at 110 rpm and slower, although there was a definite agitation of the flask contents, the swirling action was such that an aggregation of cells was formed in the center of the flasks. At shaking speeds greater than 110 rpm, the mixing action was sufficient to disperse this central aggregation. The negative effect of shaking at 100 and 110 rpm on growth would probably have been greater if this concentration of cells into a relatively unagitated central area had not occurred.

Since continuous shaking at 125 rpm and faster caused cell death, it was of interest to determine the effects of intermittent shaking. Cells were grown with shaking at 140 rpm for 30 min/day, and at 125 rpm for 15 min/6 h and 15 min/2 h. The growth curves are shown in Fig. 2. The generation times in control cultures (no shaking) were 3.4 and 3.5 days. In cultures shaken for 30 min/day at 140 rpm (curves not shown), they were 4.1 and 4.4 days. In cultures shaken for 15 min/6 h at 125 rpm they were 6.3 and 6.4 days, and for 15 min/2 h at 125 rpm the generation time in one flask was 10.9 days after a lag period of about 12 days, while cells in the duplicate flask died. Although the agreement between these two duplicate treatments was not good, the results are adequate to show that growth under these conditions is slow, and shaking for 15 min/2 h causes a considerably greater inhibition of growth than does shaking for 15 min/6 h. A lag phase occurred in all flasks in these experiments, but

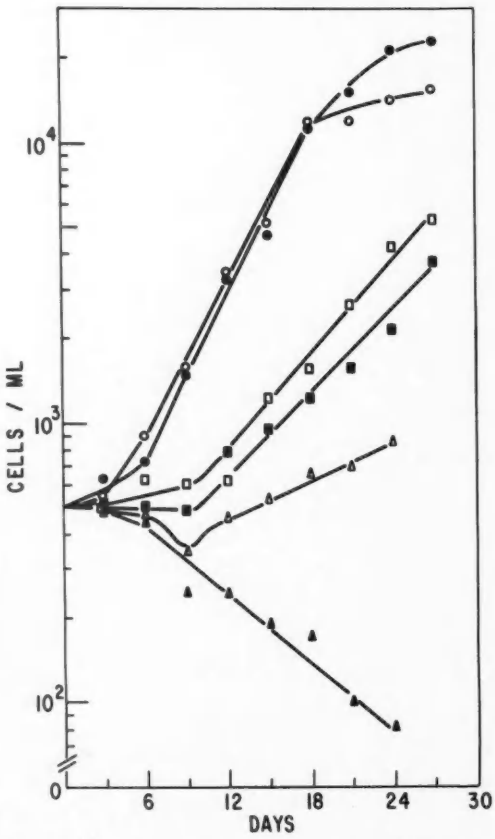

FIG. 2. Growth of *G. excavata* without shaking (●, ○) and with intermittent shaking at 125 rpm for 15 min every 6 h (■, □) and for 15 min every 2 h (▲, △).

the lag was more pronounced in the shaken cultures than in the controls.

Organic "conditioning" of the medium may be important in initiating growth in *G. excavata* cultures because the cultures show a variable lag period. It was thought that the effects of shaking might be different if cells were grown in "preconditioned" medium. To test this, a "preconditioned" medium made with the filtrate of a culture of *G. excavata* in late log phase was used. As well as making medium with the unaltered filtrate, medium was made with filtrate treated overnight with activated charcoal to remove the organic excretion products. Cells were grown without shaking and with continuous shaking at 130 rpm in these two media.

The presence of excretion products in the medium had little effect on the growth of *G. excavata* in shaken or nonshaken cultures. In both the filtrate and the charcoal-treated filtrate cell death and disintegration in the shaken cultures was as rapid as that shown in Fig. 1.

Discussion — Results show that moderate shaking of *G. excavata* cultures inhibits growth, and stronger shaking causes death and disintegration of cells. An inhibitory effect of agitation has been noted for other dinoflagellates (Galleron 1976; Tuttle and Loeblich 1975) and for certain diatoms (Schöne 1970; R. R. L. Guillard personal communication) and blue-green bacteria (Fogg and Than-Tun 1960; Volk and Phinney 1968). Although the reason for the inhibition is unknown, shaking may disturb *G. excavata* either by physically affecting cell integrity, by dispersing and disorienting cells so that phototaxis, vertical migration, and swarming are impossible, or by influencing physiological processes. At shaking speeds at which cell numbers decline and cells disintegrate (i.e. greater than about 115 rpm), the physical effects of shaking on cell integrity are certainly dominant. Schöne (1970), using cultures of marine diatoms, demonstrated an effect of agitation directly related to the physical motion itself, namely, the breaking of cell chains. Also, it has been suggested that turbulence can disrupt the colonies of trichomes of tropical marine *Oscillatoria* sp., reducing nitrogen fixation rates and thus the organism's ability to form blooms (Carpenter and Price 1976).

The growth inhibition at moderate shaking speeds may be due to processes more indirectly and subtly related to water movement than is cell integrity. For example, effects of disturbance or elimination of phototaxis, vertical migration, and swarming in dinoflagellates are unknown, but turbulence may exert its inhibitory action on growth in this mode to some degree. Also, as has been shown for certain marine diatoms, agitation may affect cell size and volume, rhythmicity of cell division, and perhaps sexual reproductive processes (Schöne 1970).

In *G. excavata* even intermittent short periods of turbulence can have marked inhibitory effects on growth rate. Shaking for 15 min at 125 rpm every 6 h nearly doubles the generation time relative to nonshaken controls. Increasing the shaking to every 2 h nearly prevents growth, and shaking for only 30 min/day causes a 20% inhibition of growth rate. Even 5 min of agitation per day affects the growth of the marine diatom *Skeletonema costatum* by causing cell division synchrony (Schöne 1970).

It is difficult to assess to what degree these results on shaking of laboratory cultures are significant in terms of natural populations and turbulent conditions in the ocean. There is not a good treatment of small-scale, oceanic turbulence (Platt 1972), and consequently not a good measure that can be used to compare turbulence in a laboratory situation to that in the ocean. Schöne (1970) has contributed to the resolution of the methodological problem with his study showing that the chain length of the filamentous marine diatom *Chaetoceros curvisetus* in nature is closely correlated with the prevailing surface sea-state. By growing *C. curvisetus* under experimental conditions in the laboratory, he is able to "measure" turbulence in terms of the corresponding sea-state, using chain length as an indicator.

Certainly large-scale turbulent phenomena in the ocean such as thermal convection cells, Langmuir cells, convergences, and perhaps internal waves and semidiurnal tides, have significant effects on the spatial structure of dinoflagellate populations and red tide formation (Kamykowski 1974; Wyatt 1975). On a smaller scale, however, pronounced turbulence, including bubble formation from cresting and breaking waves, may possibly affect potential red tide populations of dinoflagellates by inhibiting growth of individual organisms, although such an extrapolation from the laboratory situation is speculative.

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Environmentally Induced Precocious Sexual Development in the Male Pink Salmon (*Oncorhynchus gorbuscha*)

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MACKINNON, C. N., AND E. M. DONALDSON. 1976. Environmentally induced precocious sexual development in the male pink salmon (*Oncorhynchus gorbuscha*). J. Fish. Res. Board Can. 33: 2602–2605.

Nine males within a group of approximately 200 pink salmon (*Oncorhynchus gorbuscha*) reared in heated sea water became sexually mature in October of the year of hatching. These mature males (average weight = 119.44 g; average length = 19.8 cm) were larger than the immature males (average weight = 92.22 g; average length = 18.9 cm but not significantly so. This is the first record of precocious development in pink salmon other than as a result of the use of exogenous gonadotropin.

MACKINNON, C. N., AND E. M. DONALDSON. 1976. Environmentally induced precocious sexual development in the male pink salmon (*Oncorhynchus gorbuscha*). J. Fish. Res. Board Can. 33: 2602–2605.

Neuf saumons roses (*Oncorhynchus gorbuscha*) mâles, parmi un groupe d'environ 200 élevés dans de l'eau de mer chauffée, atteignirent la maturité sexuelle en octobre de l'année

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d'éclosion. Ces mâles mûrs (poids moyen = 119.44 g; longueur moyenne = 19.8 cm) étaient plus grands que les mâles immatures (poids moyen = 92.22 g; longueur moyenne = 18.9 cm) mais les différences ne sont pas significatives. C'est la première mention de développement précoce chez le saumon rose, autre que celui résultant de l'emploi de gonadotrophine exogène.

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In the course of studies on 1-yr-old male pink salmon (*Oncorhynchus gorbuscha*) reared in heated sea water, a small proportion of the males attained sexual maturity. As there is no previous record of precocity occurring naturally in this species, and in view of its possible implications for populating rivers with pink salmon in the off year, the incident and the conditions under which it occurred are reported here.

Materials and methods — Pink salmon fry were obtained from Mr F. C. Withler, Pacific Biological Station, Nanaimo, B.C., in early February 1974. These fish had been incubated and reared at an elevated water temperature (12 C) at the Nanaimo Laboratory from eggs taken at Jones Creek (near Hope, British Columbia), in October 1973. They were acclimated to salt water from January 8 to 21 before being transferred to West Vancouver. There the fish were reared outdoors under natural light in 4000-liter saltwater tanks in which flow and temperature were maintained at 30 liters/min and 12 C.

Feeding commenced January 3, using frozen brine shrimp. Beginning January 9, a wet food (Donaldson and McBride 1967) was included in the diet, and brine shrimp were deleted on January 18. Commencing January 28, the fish were fed to satiation 2 times/day a diet of Oregon Moist Pellets (Westgate et al. 1964).

On October 10, 1974 all fish exhibiting signs of male secondary sexual characteristics were sampled along with a random sample of fish exhibiting no secondary sexual characteristics. Only a small number of fish exhibiting no secondary sexual characteristics were sampled.

Sampled fish were weighed to the nearest 0.1 g and killed by decapitation. One gonad was weighed to the nearest milligram, while the other was removed, fixed in Bouin's solution, then dehydrated and embedded in paraplast, mp 56–57 C (Culling 1963). The specimens were then sectioned longitudinally at 6 μ and stained with Mayer's hematoxylin and eosin.

The gonadosomatic index (GSI) was determined as follows:

$$GSI = ([\text{wt of one gonad}] \times 2) \times 100/\text{body wt}$$

The state of sexual maturity of the testis was determined from examination of a single median sagital section from each specimen. The degree of maturity was estimated on the basis of six distinct histological stages of testicular development as defined by Funk and Donaldson (1972) in their assessment of the reproductive maturity of pink salmon: 1) spermatogonia only are present, 2) spermatogenesis has been initiated and the predominant cell types are primary spermatocytes, 3) primary spermatocytes, secondary spermatocytes, and spermatids are all present, 4) spermatogenesis is proceeding actively; spermatozoa are present in the lobule lamina and the testis reaches its maximum size, 5) the functionally mature testis shows extensive breakdown of testicular morphology with spermatozoa lying free in the sperm duct (semen can be stripped from the fish at this stage), and 6) the testis is completely regressed.

Results and discussion — Nine 1-yr-old male pink salmon in a stock of approximately 200 (sex ratio ~ 1:1) exhibited noticeable secondary sexual characteristics. Table 1 compares characteristics of these precocious males to those of males from the same stock exhibiting no secondary sexual characteristics. Both testicular weight and gonadosomatic index are significantly higher in the group displaying secondary sexual characteristics. Testes of the group showing no secondary sexual characteristics contained only spermatogonia, while testes of the maturing group showed extensive breakdown of testicular morphology with spermatozoa lying free in the sperm duct. According to the six distinct histological stages of testicular development, the maturing group was comprised of three, stage 4 fish and six functionally mature stage 5 fish, while all the fish of the immature group were functionally immature stage 1 fish.

One of the characteristics of pink salmon is a rigid 2-yr life cycle that terminates in sexual maturation, spawning, and subsequent death. Although previous studies (Donaldson et al. 1972; Funk and Donaldson 1972) have shown that male pink salmon can be stimulated to reproductive maturity 1 yr earlier than normal using exogenous piscine gonadotropin, this report is the first recorded incident of precocious maturation occurring in pink salmon without its use.

Although the data available do not establish conclusively the reason for precocious development of the nine male pink salmon, the elevated water temperature was probably responsible. Because the sexually mature fish were larger but not significantly larger than the immature fish, the maturation process may be size-dependent. That portion of the stock that exhibited the fastest

TABLE 1. Body weight, body length, gonad weight, gonadosomatic index (GSI), condition factor, and testicular stage of two sexually distinct groups of 1-yr-old pink salmon (*Oncorhynchus gorbuscha*) males from the same stock. NS = not significant.

		Mean ± 1 SD					
Group	*n*	Body wt (*g*)	Standard length (*cm*)	Gonad wt (*g*)	GSI	Condition factor (*K*)[a]	Testicular stage
1. Sexually mature	9	119.44±28.70	19.8±1.2	4.14±1.59	6.77±1.40	7.15±0.84	4.67±0.16
2. Sexually immature	5	92.22±21.31	18.9±0.8	0.02±0.00	0.04±0.01	6.48±0.066	1.00±0.00
t-test of significance		NS	NS	$P < 0.001$	$P < 0.001$	NS	$P < 0.001$

[a] $K = \frac{\text{body weight}}{\text{standard length}^{3.25}} \times 1000$

growth rate at 12 C may have reached the critical size for initiation of gonadal development. Once gonadal development has been initiated, the photoperiod regime may have been conducive to promoting further sexual development. Those pink salmon that did not reach this critical size at the time when the photoperiod was conducive would have undergone no sexual development. This may explain the "all or none" nature of sexual development observed in our fish.

Several authors have found a relationship between size and age at first maturity (Allen 1967; Ritter 1975; Wagner 1967; Donaldson 1969; Burrows 1970). Concerning species of Pacific salmon, Donaldson (1969) and Burrows (1970) working on hatchery-reared coho (*O. kisutch*) and sockeye (*O. nerka*) salmon have been the only ones to show findings similar to ours. They found that the larger the smolt the earlier it tended to mature.

There may be genetic differences within pink salmon that affect the onset of sexual maturity. Although some authors have suggested that the two "separate lines" of pink salmon (even and odd year) are genetically distinct (Ricker 1972; Neave 1952), results presented here indicate that in certain instances of special environmental conditions the possibility does exist that genetic flow could occur between the two lines of pink salmon.

The use of heated sea water to induce precocious sexual maturation might be used as a method for repopulating "off-year" cycles of pink salmon by fertilizing normal "on-year" donor eggs with the "off-year" milt collected from the precociously matured "on-year" male pink salmon natal to the river.

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Transatlantic Migrations of Spiny Dogfish (*Squalus acanthias*)

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TEMPLEMAN, W. 1976. Transatlantic migrations of spiny dogfish (*Squalus acanthias*). J. Fish. Res. Board Can. 33: 2605–2609.

The first record of a west to east transatlantic migration of a tagged spiny dogfish (*Squalus acanthias*) is reported, 11 yr after liberation at St. Pierre Bank to recapture in the Shetland Isles–northern North Sea area. The most northward and eastward records of spiny dogfish in the northwest Atlantic are presented and discussed in relation to the probable frequency of transatlantic migration. It is concluded that transatlantic migration is not great but probably not highly unusual.

TEMPLEMAN, W. 1976. Transatlantic migrations of spiny dogfish (*Squalus acanthias*). J. Fish. Res. Board Can. 33: 2605–2609.

Il s'agit de la première mention d'une migration transatlantique d'ouest en est d'un aiguillat commun (*Squalus acanthias*) marqué sur le banc Saint-Pierre et recapturé 11 a. après sa remise en liberté aux Shetland, dans la région septentrionale de la mer du Nord. L'auteur rappelle les signalements les plus au nord et les plus à l'est de l'aiguillat commun dans l'Atlantique Nord-Ouest et il les analyse en relation avec la fréquence probable de migrations transatlantiques. Il en conclut que les migrations transatlantiques ne sont pas très communes, mais qu'elles ne sont pas tellement hors de l'ordinaire.

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A spiny dogfish (*Squalus acanthias*) tagged off Newfoundland was recently recaptured in the eastern Atlantic. This dogfish was tagged on June 6, 1963 from a bottom otter-trawl catch on the northwestern slope of St. Pierre Bank, 46°21′N, 57°17′30″W in 176–212 m. The laminated plastic tag was of the Petersen disc type, 12.7 mm diam, attached through the cartilage at the base of the first dorsal spine with 0.8 mm diam stainless steel wire (type 316 soft).

The tag was returned on October 14, 1974. It was found on a dogfish landed at Måløy, Norway, by the Norwegian longliner *Skaar Senior* which had been fishing during the 1st wk of September 1974 in the Shetland–northern North Sea spiny dogfish fishing area (probably the fishing grounds east of the Shetland Isles, Fig. 1). When tagged, the fish was 74 cm in greatest total length, i.e. with the caudal fin extended directly backward. It was a female and probably immature. On recapture 11 yr later, its length was reported as 87 cm and its weight (presumably gutted) was 2.3 kg.

Related migrations and distributions — Although this is the first report of a complete west to east migration of a spiny dogfish across the

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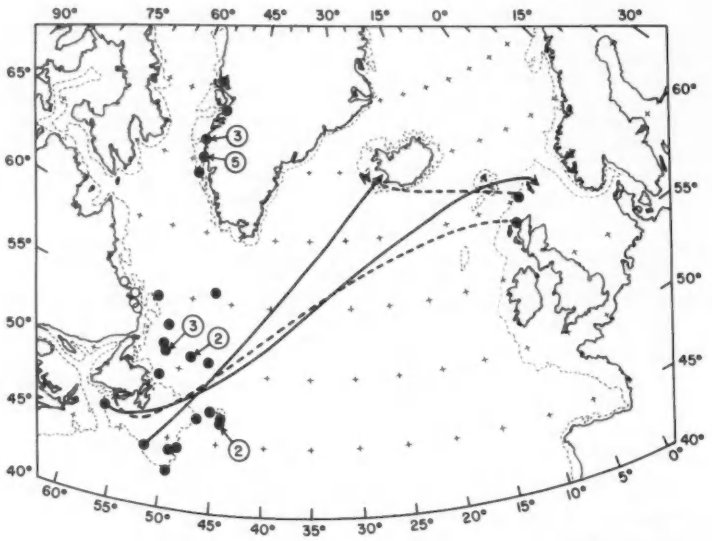

FIG. 1. Transatlantic migrations of tagged spiny dogfish (*Squalus acanthias*) and the most northward and eastward records of spiny dogfish in the northwest Atlantic. Black dots represent locations of capture of individuals, except where numerals indicating numbers taken are attached. The Labrador coastal records (○) are the most northward only and represent indefinite, probably small, numbers for the southern records and much scarcer for the northern. Solid lines show eastward transatlantic migrations of tagged dogfish from points of tagging (●) to points of recapture (arrows). Dashed lines represent the longest westward migrations. Depth contour, 183 m.

Atlantic, a 10-yr migration from Newfoundland waters to southwest Iceland was previously reported (Templeman 1958) (Fig. 1) for a female spiny dogfish 73 cm greatest total length on tagging and 79 cm natural length (ca 81 cm greatest total length) on recapture.

Holden (1967b) reported a 4-yr east to west transatlantic migration of a male spiny dogfish from north of Scotland, off Cape Wrath, to Hermitage Bay, Newfoundland, and a 5-mo migration of a spiny dogfish from north of Scotland to southwest of Iceland (Fig. 1). The longest migration recorded within the western Atlantic was from St. John's, Newfoundland, to off Cape Henry, Virginia (Templeman 1954).

The transatlantic migrations raise the questions of the frequency of these occurrences and whether or not there is enough intermingling to maintain the genetic unity of the North Atlantic populations of spiny dogfish. The questions cannot be completely answered but some evidence is available.

In the Newfoundland area spiny dogfish are often abundant coastally and on the slopes of St. Pierre Bank and southwestern Grand Bank, but otherwise scarce, at least in bottom trawling, on the Grand Bank. There is no evidence that young dogfish are born in the Newfoundland area, as the smallest in about 4000 measurements was 51 cm in greatest total length (Templeman 1944, 1963). Spiny dogfish migrate northward to the Newfoundland area in late spring and early summer. The mature females, carrying young, and most of the mature males migrate southwards in late autumn and early winter to U.S. waters where the young are born. Many immatures of both sexes and some mature males remain over winter at the southern slopes of the Grand Bank and St. Pierre Bank, and in the deep water of some Newfoundland bays where they may be killed by cold (Templeman 1944, 1963, 1965).

In coastal Labrador waters spiny dogfish are not usually numerous but have been reported:

northward to 53°30′N (Templeman 1944); to Gready, 53°50′N (Backus 1957); and by fishermen to Makkovik, 55°05′N, where they were very rare, and more plentiful at Smokey, 54°28′30″N. (Templeman 1963), (Fig. 1).

East of southern Labrador and northeast of Newfoundland the most northward capture on the continental shelf was on August 19, 1962 on Hamilton Bank at 54°45′30″N, 54°28′W. Four specimens were taken near the surface over oceanic depths: the most northward on July 19–20, 1965 at 55°45′30″N, 47°14′W, 3400 m; 2 on April 15–16, 1966 at 50°58′N. 49°00′W, 2130 m; and 1 on April 21, 1970 at 50°40′30″N, 46°57′00″W, 2900 m.

At West Greenland spiny dogfish are rare but there are at least 10 coastal (including fjord) records (7 in 1931–47 and 3 earlier; Jensen 1948; Hansen 1949). The one offshore and most southern record (Krefft 1962) is from Fylla Bank in October 1960 (Fig. 1). The most northerly record is an 820-mm female taken June 15, 1936 near Ikerassak in Umanak Fjord, ca 70°30′N (Jensen 1948).

Spiny dogfish are abundant off Iceland, especially along the south and west coasts (Saemundsson 1949). The tagged spiny dogfish migrating to Iceland from Newfoundland was one of a large school migrating into Faxa Bay, southwest Iceland (Templeman 1958).

Spiny dogfish are also common at the Faroes (Joensen and Tåning 1970) and are abundant north of Scotland, around the Shetland Isles, and off southern Norway (Holden 1965, 1967a).

Distant migrants and sexual maturity — In the Newfoundland area (Templeman 1944), the smallest of 792 mature females was 74 cm (6% of individuals mature) and the largest of 273 immature females 88 cm (98% of individuals mature) in greatest total length. The 50% mature level was between 78 and 79 cm. The smallest of 659 mature males was 60 cm long and the largest of 34 immature males 69 cm, with the 50% mature length about 64 cm.

Of 9 distant records of spiny dogfish (apart from tagged migrants) from the Newfoundland and oceanic areas (Fig. 1) examined for sex, 8 were females. Of 6 examined for sexual maturity, 1 male (75 cm) and 5 females (77–87 cm and including 3 from over oceanic depths) were all immature. The eastward migrant to Iceland was a 73-cm female at release and apparently still immature on recapture 10 yr later at 81 cm greatest total length (Templeman 1958). The eastward migrant to the Shetland Isles was a 74-cm female, almost certainly immature at release.

The most likely hypothesis is as follows: the large female spiny dogfish carrying young return south where they give birth. The mature males also mainly return southward where they mate with the females after the young are born. Only the larger dogfish, above 50 cm and mainly over 60 cm, move north to the Newfoundland area. The immature females of the Newfoundland area are larger, more numerous, and on the average less sexually mature than the immature males (Templeman 1944). They therefore are less likely to return southward and are more likely to stray over the ocean area to the north and east and remain there over winter. If they wander far enough, some of them lose their sense of direction for returning to their southward area of origin.

Of the westward migrants, that to Hermitage Bay, Newfoundland, was a 78-cm mature male on release (Holden 1967b) and the migrant to Iceland was an immature female on release (Holden 1967a).

Six of the 7 dogfish sexed from West Greenland were large females (Jensen 1949; Krefft 1962). The embryos in one female on August 28 were 285–290 mm long and in another female on September 11, 265–280 mm long. The yolk sacs in the latter were completely used up and thus they were ready for birth. The larger embryos from the other female must have been close to the end of their development. The largest embryos in spiny dogfish females in the Newfoundland area were 205 mm long in August, 230 mm in September, and 255 mm in November (Templeman 1944); they possessed yolk sacs and were not ready for birth. The much longer embryos, almost fully developed at West Greenland in August and early September, therefore, presumably did not belong to the North American stock. At Plymouth, England, the largest spiny dogfish embryos were 280 mm long in August, 290 mm in September, and 300 mm in November. The embryos were ready for birth in November–December and some as early as the end of August and in September (Ford 1921).

Temperature relationships — All 4 spiny dogfish caught in the Newfoundland area beyond the continental shelf were taken by surface gear set for Atlantic salmon (Templeman 1967, 1968; May 1972). Water temperatures in the upper 100 m of this oceanic area, where dogfish were scarce but not rare, ranged from 3.7 to 5.4 C in April and from 4.2 to 8.6 C in July.

Off Labrador there are records only from the

warmer southern part of the coast and spiny dogfish have not been recorded from the colder water north of the area where surface sea temperatures in 1928 and 1950 were about 6 C in July–August (Smith et al. 1937; Hachey et al. 1954). The most northerly Labrador records are from occasional years when the surface layer was presumably warmer than usual.

At Iceland spiny dogfish are very abundant on the south and west coasts, appear irregularly at the northwest coast and the western part of the northern coast, and are rare on the northeast and east coasts (Saemundsson 1949). Thus, they are most abundant on the warmest part of the coast. Mean sea temperatures at 20 m in August 1950–60 in rectangles near the coast were between 10 and 11.3 C southwest of Iceland, 6.8 and 7.9 C north, and 6.6 and 7.8 C east of Iceland (Stefánsson 1962).

At West Greenland the few records are mainly from the warmer section of the coast where, however, surface temperatures in summer are lower than north of Iceland (Hermann 1959, 1969, 1972).

It is likely that, especially in winter, the oceanic North American spiny dogfish keep to the warmer water south of Greenland and are more likely to move toward western Iceland and northern Scotland than toward Greenland.

Taggings and recaptures — From the tagging of 2,855 spiny dogfish off Newfoundland in 1942–65, 8.2% were recaptured (Templeman 1954; and unpublished data). Jensen (1969) recorded the tagging of 907 spiny dogfish in the New England area in 1956–64, with 3.0% recaptures. Shafer (1970) reported 1.7% recaptures from the tagging of 3,583 spiny dogfish from off Nova Scotia to Wimble Shoals (north of Cape Hatteras, North Carolina) in 1966–69. The longest migration recorded was from off Block Island, Rhode Island, to off Mayport, Florida, a distance of 1120 naut. miles, in 98 days. Shafer noted that additional tagging was being carried out.

Holden (1965) reported 8.3% recaptures from 12,063 spiny dogfish tagged in the northeast Atlantic by British scientists, 1957–62, and Aasen (1964a, b) reported 10.8% recaptures from 8,122 tagged in the northeast Atlantic by Norwegian scientists in 1958–63. Holden (1967a) said that more than 13,000 spiny dogfish were tagged by the British and over 10,000 by the Norwegians.

The percentage recaptures quoted above are usually quite minimal because many tags were still being returned at the time of reporting. Even from the 2,395 dogfish tagged off Newfoundland in 1962–65, occasional recaptures are still being made. From the taggings off Newfoundland, including the long eastward journey to Iceland as transatlantic, 2 of the reported 234 recaptures made transatlantic journeys. The 2 longest migrations westward were from 1929 reported recaptures. The westward journey to Iceland was relatively short and only one of these westward migrations could be classed as transatlantic.

Population size and possibilities of transatlantic migration — Only recently have large commercial catches of dogfish (*Squalus* and *Mustelus* spp. in the statistics, but mainly *S. acanthias*) been made in the western Atlantic (ICNAF subareas 1–6). Landings in 1974 were 24,552 metric tons, probably at least 15 million fish. Landings rose from 17,388 tons in 1973 and 697 tons in 1972 (ICNAF 1974–76). In the Newfoundland area (ICNAF subarea 3) from which the transatlantic migrations eastward originated, 126 tons of spiny dogfish, probably more than 90,000 fish, were taken in 1974. Templeman (1963) reported large research catches of spiny dogfish in late May–early June on St. Pierre Bank, the largest over 8,300 fish in a ½-h set, and Templeman (1944) also reported a subsidized catch of 2–3 million spiny dogfish in the coastal waters of Placentia Bay, Newfoundland, in 1938. There were therefore large numbers of spiny dogfish available in suitable locations to begin transatlantic migrations.

Large landings of spiny dogfish from the northeast Atlantic began earlier. In the statistics for the northeast Atlantic (ICES Bulletin Statistique), dogfish landings are reported differently by various countries, some reporting under "picked dogfish" (spiny dogfish) and others under "dogfishes and hounds." Almost all the landings of the latter category are evidently also spiny dogfish. Total landings in both categories from the northeast Atlantic reached a peak of 63,718 metric tons in 1963 and gradually declined to 44,800 metric tons in 1973. Of the 1963 landings, 62%, and of the 1973 landings, 77%, were reported as spiny dogfish. For the remainder, the English landings in 1963 and the English and Welsh landings in 1973 were 7 and 18% of the overall total of all dogfishes (Holden 1967a; ICES 1966, 1976). Approximately 99% of the English landings, all reported as "dogfish and hounds," consist of spiny dogfish (Holden 1967a). A large proportion of these landings came from the Scottish–Norwegian stock from which the westward transatlantic migrant came. Large numbers

are therefore present in a favorable location for transatlantic migration westward by way of the Faroes and Iceland.

Transatlantic migration is apparently not great but also probably not highly unusual.

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Residue Dynamics of Di-2-ethylhexyl Phthalate in Fathead Minnows (*Pimephales promelas*)[1]

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MAYER, F. L. 1976. Residue dynamics of di-2-ethylhexyl phthalate in fathead minnows (*Pimephales promelas*). J. Fish. Res. Board Can. 33: 2610–2613.

Fathead minnows (*Pimephales promelas*) were continuously exposed to 1.9–62 μg/liter di-2-ethylhexyl phthalate (DEHP) for 56 days. The accumulation factors ranged downward from 886 to 155 as the exposure concentrations increased. The major metabolite of DEHP was the monoester, 2-ethylhexyl phthalate. After being placed in uncontaminated water, the fish eliminated half of the DEHP in 12.2 days.

MAYER, F. L. 1976. Residue dynamics of di-2-ethylhexyl phthalate in fathead minnows (*Pimephales promelas*). J. Fish. Res. Board Can. 33: 2610–2613.

Nous avons exposé de façon continue des têtes-de-boule (*Pimephales promelas*) à 1.9–62 μg/litre de di-2-éthylhexyl phthalate (DEHP) durant 56 jours. Les facteurs d'accumulation vont en diminuant de 886 à 155 à mesure que les concentrations d'exposition augmentent. Le métabolite principal du DEHP est le monoester, 2-éthylhexyl phthalate. Une fois transférés dans de l'eau non contaminée, les poissons éliminent la moitié du DEHP en 12.2 jours.

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DI-2-ETHYLHEXYL phthalate (DEHP) is the most widely used plasticizer in polyvinyl chloride plastics (U.S. Tariff Commission 1972), and the finished plastic product may contain up to 60% of DEHP by weight (Nematollahi et al. 1967). The ubiquity of DEHP as a contaminant in various constituents of aquatic ecosystems was described by Mayer et al. (1972). DEHP has also been reported to occur naturally (Mathur 1974a).

The toxicity of DEHP and its effects on reproduction in aquatic organisms were described by Mayer and Sanders (1973) and Sanders et al. (1973), and DEHP degradation in fishes was evaluated by Metcalf et al. (1973) and Stalling et al. (1973). DEHP has been found degradable in soil (Mathur 1974b), sediments (Johnson and Lulves 1975), sludge (Saeger and Tucker 1973), and by an almost ubiquitous bacterial saprophyte (Mathur and Rouatt 1975). Because little is known of the residue dynamics of DEHP in fishes, the present study was undertaken to elucidate the uptake, storage, degradation, and elimination of the chemical in the fathead minnow (*Pimephales promelas*).

Materials and methods — The study was conducted in a flow-through diluter system modified from Mount and Brungs (1967) and consisted of seven concentrations of DEHP (1.9, 2.5, 4.6, 8.1, 14, 30, and 62 μg/liter) and a control. Exposure containers were glass aquaria, 61 × 30.5 × 30.5 cm, containing 42 liters of well water (pH 7.4, total hardness 270 mg/liter as $CaCO_3$) maintained at 25 ± 0.5 C. Stock solutions of ^{14}C-carbonyl-labeled DEHP (1.64 mCi/mmol) mixed with nonlabeled DEHP were prepared in acetone to give a specific activity of 180 cpm/μg. The amount of acetone did not exceed 0.25 ml/liter in the exposure vessels. DEHP concentrations in the exposure water were monitored radiometrically at weekly intervals by extracting 1-liter water samples with diethyl ether.

Sixty fathead minnows, 7.5 mo old and each weighing 1.24 g (± SD 0.31) were placed in each of eight aquaria; seven of the lots were continuously exposed to different concentrations of DEHP for 56 days. After the exposure, the fish were placed in uncontaminated water for an additional 28 days. The fish were maintained, in general, according to the methods described by Brauhn and Schoettger (1975), and fed a commercial trout starter (EWOS) throughout the study.

Four fish were removed from each concentration and from the control for total radioactivity deter-

[1]Information contained herein and/or mention of products by commercial or trade names does not constitute endorsement by the U.S. Department of the Interior, Fish and Wildlife Service, Fish–Pesticide Research Laboratory.

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TABLE 1. Total ^{14}C carbonyl-labeled di-2-ethylhexyl phthalate (micrograms per gram) in fathead minnows (*Pimephales promelas*) held at 25 C during periods of uptake (days 1–56) and elimination (days 57–84); standard errors in parentheses.

	Mean exposure concn[a] (*μg/liter*)						
Days	1.9 (0.1)	2.5 (0.1)	4.6 (0.2)	8.1 (0.2)	14 (0.6)	30 (0.7)	62 (3)
1	0.26 (0.02)	0.40 (0.05)	0.48 (0.04)	1.2 (0.1)	1.4 (0.1)	1.8 (0.1)	2.1 (0.1)
3	0.46 (0.09)	0.77 (0.08)	1.0 (0.1)	1.8 (0.1)	2.6 (0.1)	3.4 (0.1)	3.1 (0.7)
7	0.70 (0.07)	0.93 (0.12)	2.2 (0.5)	2.9 (0.5)	3.3 (0.2)	3.2 (0.3)	3.9 (0.1)
14	0.87 (0.12)	1.5 (0.2)	2.6 (0.2)	2.8 (0.2)	2.7 (0.2)	3.2 (0.4)	3.8 (0.6)
28	1.4 (0.2)	2.2 (0.1)	3.1 (0.5)	2.9 (0.4)	4.8 (0.6)	7.5 (0.9)	6.9 (1.9)
56	1.4 (0.1)	2.2 (0.1)	4.1 (0.6)	3.6 (0.4)	5.0 (0.7)	8.6 (0.5)	9.6 (0.6)
63	0.73 (0.29)	0.95 (0.02)	1.9 (0.2)	1.9 (0.1)	2.7 (0.4)	3.2 (0.7)	9.6 (1.4)
70	0.38 (0.11)	0.64 (0.10)	1.1 (0.1)	1.3 (0.3)	1.1 (0.1)	1.7 (0.2)	7.8 (0.6)
84	0.32 (0.06)	0.28 (0.05)	0.54 (0.04)	0.73 (0.12)	1.2 (0.1)	1.8 (0.3)	4.2 (0.6)
Half-life (*days*)							
^{14}C	13.6	9.7	10.0	12.6	14.7	12.8	21.6
DEHP	14.2	6.2	6.2	11.8	13.3	15.4	18.3

[a]No background residues of DEHP were found in the control water or fish.

minations after 1, 3, 7, 14, 28, and 56 days of exposure and after 7, 14, and 28 days in uncontaminated water. Total radioactivity in each fish was determined after Rodgers and Stalling (1972). DEHP and its degradation products were analyzed by thin-layer chromatography (Stalling et al. 1973) on pooled samples of four fish each after 28 and 56 days of exposure, and after 7, 14, and 28 days in uncontaminated water. In addition, DEHP was determined in each of the pooled samples by gas-chromatographic analyses (Stalling et al. 1973).

Accumulation factors were determined by dividing the concentration in the fish (micrograms per gram, wet weight) by the concentration in the water (micrograms per liter) times 1000. Predicted equilibria (asymptotes) of total radioactivity in the fish were derived by fitting the observed data to a Gompertz curve (Croxton and Cowden 1955). The half-life of DEHP was determined by the method of Chase and Rabinowitz (1967) and the effect of concentration on accumulation factors was analyzed by linear regression ($\log Y = a + b \log X$).

Results and discussion — The fish accumulated 1.4 and 9.6 μg/g of DEHP residues after 56 days of exposure in the 1.9- and 62-μg/liter concentrations, respectively (Table 1). The accumulation factors of 34–137 times the water concentration observed after 24 h exposure in fathead minnows agree well with the factors of 35–92 times observed by Metcalf et al. (1973) in the guppy (*Lebistes reticulatus*). Equilibria of ^{14}C-DEHP in fathead minnows were approached between 28 and 56 days of exposure. From the predicted equilibrium concentrations (1.5, 2.3, 3.7, 3.2, 5.2, 9.8, and 9.2 μg/g), residues in fish exposed to 1.9 and 2.5 μg/liter approached equilibria at 28 days, 4.6 and 8.1 μg/liter at 42 days, and 14, 30, and 62 μg/liter at 56 days.

Accumulation factors at 56 days ranged from 155 to 886 for total ^{14}C, and from 91 to 569 for DEHP (Fig. 1), and decreased as exposure concentrations increased. Accumulation factors are now commonly being used in assessing the propensity of a chemical to accumulate in aquatic organisms, with little or no consideration of the effects of concentration in the surrounding medium. The present data indicate that large errors

TABLE 2. Percentage composition of ^{14}C-labeled residues in fathead minnows after 56 days of continuous exposure to ^{14}C-carbonyl-labeled di-2-ethylhexyl phthalate.

Exposure concn (μg/liter)	Residue					
	DEHP[a]	MEHP[b]	Phthalic acid	MEHP conjugate[c]	Phthalic acid conjugate[c]	Other[d]
1.9	79	12	2.5	4.1	1.2	1.2
2.5	70	24	1.7	2.2	1.1	1.0
4.6	69	23	4.1	1.2	0.6	2.1
8.1	70	21	5.4	1.0	1.2	1.4
14	60	30	3.6	0.6	5.1	0.7
30	42	40	11	0.4	6.6	0.3
62	33	50	5.7	0.4	9.8	1.1

[a]Di-2-ethylhexyl phthalate.
[b]2-ethylhexyl phthalate.
[c]Glucuronid conjugates of MEHP and phthalic acid.
[d]Unidentified material remaining at origin during thin-layer chromatography.

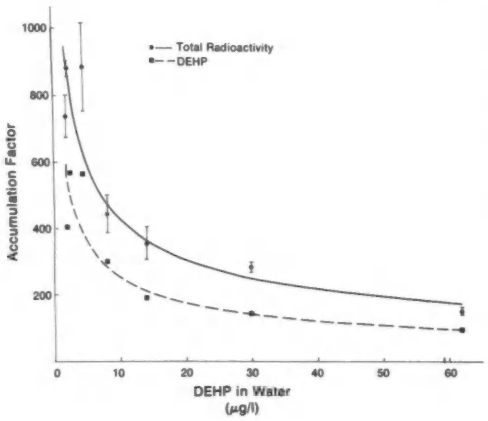

FIG. 1. Effect of concentration on the accumulation of ^{14}C-carbonyl-labeled di-2-ethylhexyl phthalate in fathead minnows (*Pimephales promelas*) after 56 days of exposure. (Total radioactivity = mean and standard error for four fish; DEHP = gas-chromatographic value of DEHP only in a pooled sample of four fish).

in deriving accumulation factors can occur if the organisms are not exposed to two concentrations having a range greater than one log interval.

Reductions in accumulation factors accompanying increases in exposure concentrations may have been due to the induction of detoxifying enzymes in the liver as reported in Hodgson (1968), and a later increase in DEHP degradation and elimination, and therefore a lower accumulation factor. This hypothesis is supported by the composition of the ^{14}C-residues at 56 days (Table 2). As exposure concentrations increased, the proportion of DEHP decreased and degradation products of the diester increased. However, half-life determinations did not substantiate the hypothesis in its entirety (Table 1). The decrease in half-life with increasing concentrations through the 4.6-μg/liter exposure, followed by an increase at higher concentrations, possibly indicated liver malfunction after 56 days of continuous exposure (liver tissues were not examined).

Although DEHP accumulated in fish, the factor of accumulation was about 1% of that observed for DDT (Metcalf et al. 1973). Fathead minnows readily degraded DEHP to 2-ethylhexyl phthalate and phthalic acid, and the half-life was relatively short, averaging 12.2 days. The disappearance of DEHP residues after the fish were placed in uncontaminated water was due mainly to degradation and elimination and not dilution resulting from fish growth. The fish at the end of the elimination period weighed 33% more than those at the beginning (day 56), and the observed DEHP concentrations at the end were 17–58% of the calculated concentrations that would have been observed if the total decrease in DEHP had been from growth. However, the presence of DEHP residues is not without biological effect. Water concentrations of DEHP as low as 3 μg/liter have caused a 60% reduction in reproduction of *Daphnia magna* (Mayer and Sanders 1973; Sanders et al. 1973). The effects of DEHP or its degradation products on growth and reproduction in fishes are not yet known.

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Postmortem Bile Damage to Rainbow Trout (*Salmo gairdneri*) Livers[1]

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Peripheral liver necrosis in rainbow trout (*Salmo gairdneri*) was shown to result from pre- or postmortem exposure to bile. Accidental spillage of bile onto the liver during sampling or intentional submersion of liver tissue into bile resulted in a time-dependent destruction of liver tissue. Awareness of this caustic property of bile should prompt extreme care in the collection of trout livers for histology.

HENDRICKS, J. D., L. J. HUNTER, AND J. H. WALES. 1976. Postmortem bile damage to rainbow trout (*Salmo gairdneri*) livers. J. Fish. Res. Board Can. 33: 2613–2616.

Nous constatons que la nécrose hépatique périphérique chez la truite arc-en-ciel (*Salmo gairdneri*) résulte d'une exposition, avant ou après la mort, à la bile. Le déversement accidental de bile sur le foie au cours de l'échantillonnage ou l'immersion intentionnelle de tissu hépatique

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dans la bile causent une destruction du tissu hépatique, qui est fonction du temps. Connaissant cette propriété caustique de la bile, on devrait être extrêmement prudent dans la collecte de foies de truite pour études histologiques.

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AFLATOXIN-induced hepatoma studies in rainbow trout (*Salmo gairdneri*) have been in progress at the Food Toxicology and Nutrition Laboratory since 1963. In the course of this work, many thousands of trout livers have been excised, weighed, examined grossly under a dissecting microscope, and fixed in Bouin's solution for later histopathological observation. Examination of stained slides has revealed the erratic occurrence of a layer of necrotic cells, of variable thickness, on the uncut edges of certain livers (Fig. 1 and 2). The cause of this peripheral necrosis has remained obscure, although some facet of our sampling procedure was suspected. Careful reexamination of many of these liver sections revealed that the necrotic rim of cells was thickest in the vicinity of the excised gallbladder. As a result, we suspected bile as the necrotizing agent and proceeded to test this possibility.

Materials and methods — Approximately 20 ml of bile was collected from the gallbladders of several yearling rainbow trout that had been reared on our experimental test diet (Lee et al. 1967). The liver from a single fish was then carefully excised to prevent bile spillage and cut into seven small pieces, each having at least two uncut edges remaining. One of these was fixed immediately in Bouin's solution and the remaining six pieces were submersed in the fish bile. Individual pieces were removed at the end of 1, 2, 5, 10, 15, and 20 min and fixed in Bouin's. Tissues were then processed by routine paraffin methods, sectioned at 6 μ, and stained with hematoxylin and eosin (H&E).

Results — As suspected, the pieces of liver that were exposed to bile showed a rim of necrotic cells identical to those we had observed before (Fig. 3 and 4). The thickness of the necrotic layer, measured by ocular micrometer, was directly time-dependent:

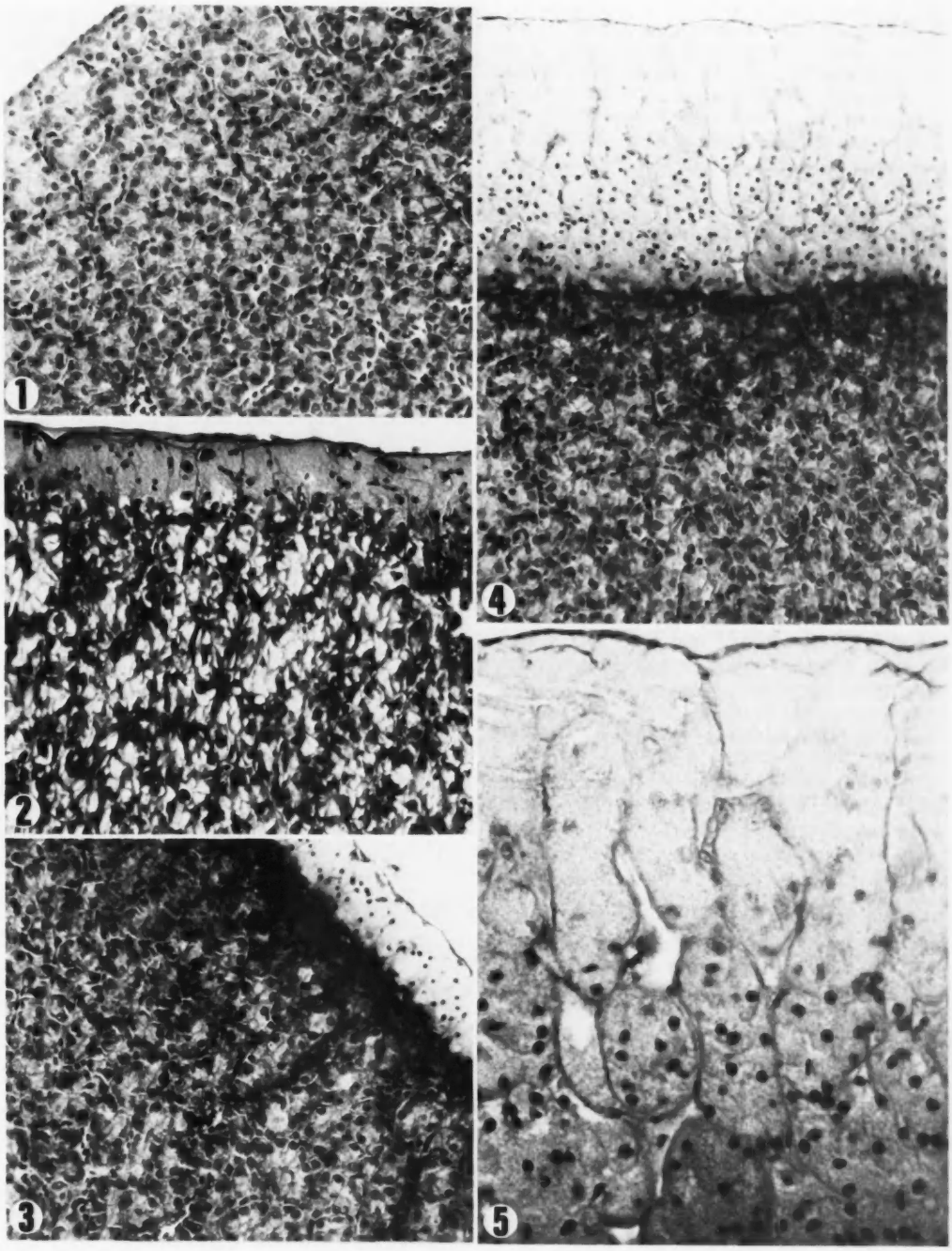
Length of exposure *(min)*	Avg depth of necrosis *(nearest 5 μ)*
0	0
1	65
2	90
5	135
10	165
15	215
20	265

The bile appeared to damage the liver cells by lysing the plasma membrane and inducing nuclear pyknosis and cytoplasmic homogenization. The end result was a granular homogeneous mass containing pyknotic nuclei and delineated only by fused remnants of the basement membranes and endothelial linings of the sinusoids (Fig. 2–5). The latter were also destroyed but retained their structural identity. Small clumps of lysed erythrocytes with pyknotic nuclei were often seen within the altered sinusoids. After prolonged exposure to bile, 15 and 20 min, the nuclei from the more peripheral cells were no longer pyknotic but were undergoing karyolysis (Fig. 5). Effects of the advancing toxic front could be seen interior to the overt necrosis. The cells in this region had lost their original shape, the nuclei were undergoing pyknosis, and the cytoplasm was granular and more basophilic (Fig. 3 and 4).

Discussion — The present experiment shows that the necrotic rim of cells which we had periodically observed on trout livers is the result of bile that accidently spills over the liver as the gallbladder is removed. The varying amounts of time involved in weighing and gross observation of the livers allows the bile to penetrate and destroy the liver cells.

Our customary practice of collecting liver samples on Monday, after the fish have been fasted over the weekend, results in the fish having full

FIG. 1. Section of normal rainbow trout (*Salmo gairdneri*) liver with a short segment of unaffected border at upper left. H&E. 383×; FIG. 2. Necrotic border on a section of liver from a routine sample at the Food Toxicology and Nutrition Laboratory H&E. 383×; FIG. 3. Section of liver showing effects of a 1-min exposure to bile. Note the wide necrotic margin at upper right, the underlying basophilic region of active cell destruction caused by the advancing bile front, and the inner unaffected liver cells. H&E. 383×; FIG. 4. Effects of a 15-min exposure to bile are shown in this liver section. The tissue destruction is similar to that in Fig. 3 but the depth of penetration is much greater. H&E. 383×; FIG. 5. Detail of the necrotic area of Fig. 4. The nuclei in the peripheral region (top) have been lysed whereas they are pyknotic in the inner region. Former hepatic cords have been reduced to sac-like masses of necrotic debris. The former basement membrane and sinusoidal walls are still intact. H&E. 952×.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gallbladders. This accentuates the problem, as it is difficult to remove the turgid organs without some spillage onto the liver. Being aware of the problem now, we are able to exercise more care in dissection and prevent this unwanted tissue damage.

The bile damage that we have described has always been seen on the surface of postmortem livers. To determine whether similar damage would occur on the surface of living liver tissue, we have exposed anesthetized, surgically opened trout livers to bile for 10 min and found similar destruction of the living peripheral liver tissue. This agrees with the observation by Sherlock (1955) that bile is toxic to human liver parenchyma when released into the tissue during acute obstructive jaundice. Our search of the literature failed to reveal any references to the caustic effects of bile on liver tissue in other animals, but we assume it would be similar to what we have seen. There also appears to be no reference in the literature concerning the components of bile that cause its caustic properties. Hunn (1969) determined the inorganic composition of rainbow trout bile, Denton et al. (1974) characterized the bile acids of rainbow trout bile, Kellogg (1975) described the bile acids of the channel (*Ictalurus punctatus*) and blue (*I. furcatus*) catfish, Boyer et al. (1976) analyzed bile from two elasmobranchs, and Oser (1965) reported the complete analysis of human bile, but none of these authors made any comment about the lytic properties of bile. Bile exerts a powerful emulsifying action on lipids in the duodenum, so it may be through a similar mechanism that it attacks structural lipids in cell membranes, causing their lysis. Consequently, we would expect bile to lyse and destroy other tissues as well as liver, although we have not determined this histologically. It would be useful to know which component(s) of bile are lytic and also what mechanisms exist to protect the liver cell tissue adjacent to the bile canaliculi and the epithelial cells of the bile duct system, gallbladder, and small intestine from the destructive effects of bile.

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Atlantic Salmon (*Salmo salar*) of the Leaf River, Ungava Bay

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LEE, R. L. G., AND G. POWER. 1976. Atlantic salmon (*Salmo salar*) of the Leaf River, Ungava Bay. J. Fish. Res. Board Can. 33: 2616–2621.

The Leaf River supports the most northerly known population of anadromous Atlantic salmon (*Salmo salar*) in Canada. River growth averaged 40–50 mm/yr, smolts averaged 258 mm fork length (range 190–300 mm) and 5.3 yr (range 4+ to 7+). Many males matured in fresh water and either incurred heavy mortality or became residual. Sex ratios among smolts were 5:1 in favor of females and among adults 3:1 in favor of females. Female 2-sea-winter salmon accounted for

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75% of the fresh-run fish. Upstream migration peaked in August: kelts were still resident in the river 11 and 12 mo later.

LEE, R. L. G., AND G. POWER. 1976. Atlantic salmon (*Salmo salar*) of the Leaf River, Ungava Bay. J. Fish. Res. Board Can. 33: 2616–2621.

La rivière aux Feuilles supporte la population la plus septentionale connue de saumons atlantiques (*Salmo salar*) anadromes au Canada. La croissance en rivière est de 40–50 mm/a. en moyenne, les smolts ont une longueur à la fourche moyenne de 258 mm (gamme de 190–300 mm), et l'âge moyen est de 5.3 a. (gamme de 4+ à 7+). Plusieurs mâles atteignent la maturité en eau douce et subissent de fortes mortalités ou encore deviennent résiduaires. La proportion des sexes chez les smolts est de 5:1 en faveur des femelles, et chez les adultes de 3:1 en faveur des femelles. La montaison en eau douce est constituée à 75% de femelles ayant passé deux hivers en mer. La migration en amont atteint un sommet en août: il reste encore des charognards dans la rivière 11 et 12 mois plus tard.

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THE Leaf River is the most northerly Canadian river in which anadromous Atlantic salmon (*Salmo salar*) are known to spawn. The river and its fish fauna were briefly described by Jessop et al. (1970). Power (1969) published an account of the salmon of Ungava Bay and information then available suggested the Leaf River contained few salmon. Verbal reports of Department of Indian and Northern Affairs officers indicate salmon are occasionally taken in the mouths of rivers to the north. Beyond this, in Hudson Bay's drainage, outside the previously known range of Atlantic salmon, Le Jeune and Legendre (1968) report the presence of relict salmon at 59°34′N, 77°18′W in the Kogaluk River.

In 1968, 64 adult and 319 juvenile Atlantic salmon were taken in the lower reaches of the Leaf River. Atlantic salmon was the fourth commonest species caught following brook trout (*Salvelinus fontinalis*), round whitefish (*Prosopium cylindraceum*), and Arctic char (*S. alpinus*) although it may not be commercially abundant. This note gives details of the salmon taken which exhibit considerable adaptation in the juvenile stages of the life cycle in response to conditions in this northern river.

Materials and methods — Fishing was carried out between June 28 and September 8, 1968, in a section of river approximately 19 km above the tidal rapids centered at 58°39′N, 70°35′W. The width varied from 200 to 900 m, depth from a few centimeters to over 8 m, current from 1 to 2 m/s, and temperature from 10 to 15 C. Data supplied by the Ministère des richesses naturelles, Québec show that the summer discharge, at this point, averages 991 m^3/s, discharge falls to a minimum of about 17 m^3/s in April and rises to a maximum in late May of 5094 m^3/s. Eight to ten monofilament nylon gillnets 8 × 1.8 m and 2–10 cm stretched mesh were used continuously, fished singly from shore in suitable bays and eddies. The lower reaches of several tributary streams were sampled with rotenone but no young salmon were obtained. All specimens were examined fresh; fork lengths were recorded in millimeters, weights in grams, and sex, states of maturity, stomach contents, and other observations were generally noted in the field. Scales were removed from the flank, above the lateral line just posterior to the dorsal fin; smears were prepared as described by Power (1964).

Results — Juveniles — Although it is customary to separate young salmon into parr and smolt, this was not done in the initial analysis. A clear separation into parr and smolts was not easy because some fish were in the process of transformation and fish killed in gillnets tend to revert to a parr-like coloration. Salmon that had not yet migrated to the sea were classified as juveniles (even though some were sexually mature); the rest were classified as adults. A length-frequency distribution of the sample of 319 juvenile salmon, separated by sex and age, was obtained (Fig. 1). The mean lengths (L), weights (W), and condition factors (k) of these fish were calculated ($k = 100\ W[g]/L^3[cm]$) (Table 1). These salmon lose their parr-like coloration and assume the smolt coloration and profile between approximately 18 and 22 cm. The change is delayed by sexual maturity.

Summer growth is not easily demonstrated with the samples available. New circuli appeared on the scales early in July and were added at the rate of about 1.5 per week in July, 1.0 per week in August, and 0.5 per week in September. This probably reflects the seasonal growth pattern. There was a marked difference between immature males and maturing males, the latter adding fewer circuli. This difference was illustrated for the 5+ age-group sample, which was the only one large enough to provide a clear result (Fig. 2). Growth of the 5+ juvenile female sample between July 1 and September 10 could be described by the equation: Length (millimeters) = $0.43X + 235$; (X = number of days since

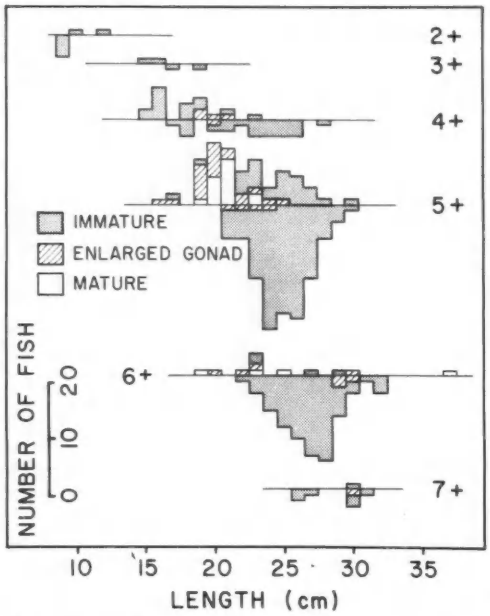

FIG. 1. Length-frequency distribution of juvenile Atlantic salmon (*Salmo salar*) from Leaf River separated by age. Males are shown above the lines, females below. Fish indicated as mature would have spawned that year; those with enlarged gonads were in the initial stages of maturation and probably would not have spawned.

July 1). Confidence intervals (95%) on the slope of this line indicated a daily increment of 0.43 ± 0.19 mm. The other age-groups were either too small or the samples were complicated by factors such as migration, residual smolts, and sexual maturity which occurred at the expense of growth in length. The slopes of the calculated growth equations were not significantly different from zero.

Adults — Fresh-run salmon were taken between July 26 and September 7. Between August 16 and 19 almost 30% of the 51 fresh-run fish were landed. This presumably corresponds to the peak period of upstream migration. Eleven salmon kelts were taken between July 7 and August 1. These were descending to the sea following the spring flood. Two delayed migrants were taken later, on August 17 and August 29, respectively.

Three classes of fresh-run salmon were present (Table 2): grilse (~12%), 2-sea-winter salmon (~86%), and previously spawned fish (~2%). The sex ratio was highly in favor of females (3:1).

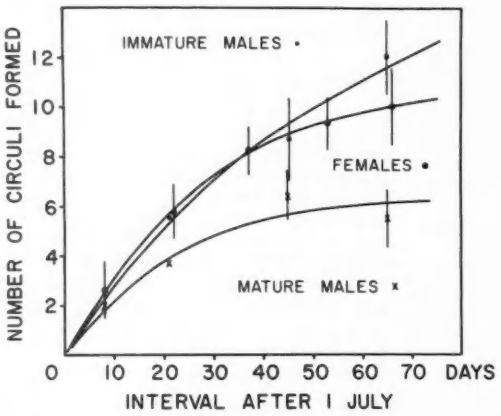

FIG. 2. Number of circuli formed on the scales of 5+ juvenile salmon from Leaf River, during the 1968 growing season. The points are means for groups of fish; 1 SD about each mean is indicated by a vertical line.

The ages at first migration to sea can be estimated from the age composition of the smolts sampled in the lower reaches of the river and from the river ages recorded on the scales of the adult fish. Parr, as recognized by their coloration and condition factor, and juvenile males with gonads in a state of development that would indicate autumn spawning were first removed from the sample of juvenile fish. The rest were assumed to be smolts in migration, although some were, and some would become, residual smolts. Table 3 records the results which, considering the small size of the samples, provide a consistent estimate of mean age at migration of 5.3 yr. If total age is calculated from the time of egg deposition in late autumn, the grilse average 7.3 yr and the 2-sea-winter salmon 8.3 yr. The oldest fish in the sample was almost 10 yr old, a female with 7 yr in fresh water and 2 sea winters.

Some data were obtained on fecundity of Leaf River salmon but it was restricted to sampling one ovary from each of 13 fish. The pooled results indicated that a salmon 802 mm long and weighing 5.539 g contains 8024 eggs which average 3.63 mm diam in late August. This gives an egg production of 1450 per kilogram body weight. Two juvenile females with enlarged gonads taken in early July, 297 and 298 mm fork length, contained 3040 and 2820 eggs, 1.21 and 1.13 mm diam, respectively.

Discussion — Observations show that Leaf River salmon are similar to those in other Ungava rivers (Power 1969) and emphasize the

TABLE 1. Mean lengths (millimeters), weights (grams), and condition factors (k) of juvenile Atlantic salmon (*Salmo salar*) from the Leaf River. ±1 SD where applicable.

Age	Sex	Length (*mm*)	Weight (*g*)	k
	2 ♂	115	16.0	1.05
2+	4 ♀	94±2	9.0±0.8	1.08
	2 ♂	159	47	1.17
3+	2 ♀	182	65	1.05
	19 ♂	185±23	71±26	1.09
4+	22 ♀	230±31	125±43	0.99
	65 ♂	226±29	127±42	1.09
5+	109 ♀	253±19	159±38	0.96
	12 ♂[a]	245±50	160±63	1.05
6+	74 ♀	274±22	199±46	0.95
	1 ♂	318	315	0.98
7+	7 ♀	296±26	229±58	0.95

[a]11 for weight and condition factor.

TABLE 2. Lengths (millimeters), weights (grams), and condition factors (k) of adult salmon from the Leaf River. ±1 SD where applicable.

Class and sex of salmon	Length (*mm*)	Weight (*g*)	Condition factor (k)
Grilse 5 ♂	613±32	2608±447	1.12±0.08
Grilse 1 ♀	681	4040	1.27
2-sea-winter 6 ♂	811±48	5860±1239	1.08±0.08
2-sea-winter 38 ♀	795±41	5489±747	1.08±0.12
Previously spawned 1 ♂	848	6910	1.13
Kelts of grilse 4 ♂	650±9	2630±367	0.94±0.09
Kelts of 2-sea-winter 9 ♂ + ♀	787±25	4251±660	0.86±0.10

TABLE 3. Age at migration to sea of Leaf River salmon based on proportion of nonmaturing smolts in each age-group sampled and on adult scale reading.

Group of fish	Age at migration 4	5	6	7	Mean age
Smolt ♂	4	30	8	1	5.1
Smolt ♀	20	109	74	7	5.3
Total smolt	24	139	82	8	5.3
Grilse	1	2	2	1	5.5
2-sea-winter	5	21	17	1	5.3
Kelts	3	8	2		4.9
Total adult ♀	5	24	17	2	5.3
Total adult ♂	4	7	4		5.0
Total adult	9	31	21	2	5.3

way in which the anadromous salmon has adapted to conditions at the northern edge of its range in Canada.

The sample of juvenile salmon contained no underyearlings or 1+ parr and only 10 fish were younger than 4+ yr. Apparently, in common with other Ungava salmon rivers, the lower reaches of the Leaf River are populated by older fish which have dispersed from nursery areas farther upstream. The river has rapids but no serious obstructions to salmon migration between the sea and Lac Minto. Although our results may be biased somewhat in favor of larger fish among the youngest age-groups, they show young salmon grow rapidly in Leaf River (Table 1). Mean lengths for different age-groups indicate an annual increment of 40–50 mm. Attempts to demonstrate the seasonal growth pattern within age-groups were not altogether successful. Addition of scale circuli (Fig. 2) indicated rapid growth during July and early August and slow growth in early September. The growing season (daily mean temperature above 5.6 C) averages 90 days (Wilson 1971). If the annual increment is averaged into the growing season, the mean daily increment lies between 0.44 and 0.55 mm. This agrees with the calculated daily increment of 0.43 ± 0.19 mm for the 5+ female fish during the growing season. The latter may be an underestimate. It is similar to those for parr in the lower reaches of the Koksoak and Whale rivers which were between

0.43 and 0.89 mm/day, during July and August (Power 1969). It should, however, be more comparable to the estimates for smolts which were between 1.30 and 1.53 mm/day in the Whale River during late July and August. The difference lies no doubt in the nature of the sample which in the Leaf River included two large residual smolts taken early in the season and a number of rather small fish taken in late August and early September. The latter may be recently metamorphosed fish which would have migrated the following year as 6+ smolts. Separation of such fish from the sample becomes an arbitrary matter and for this reason the fish were grouped by age only. The 6+ age-group was similarly rather heterogeneous which explains the lack of correlation between length and date of capture. The point to be made, however, is that even at the latitude of Leaf River, growth of juvenile salmon is rapid during the brief growing season.

The smolts that migrate from Leaf River are old (mean age 5.3 yr, Table 3) and large: the mean length of the 253 fish classified as migrating smolts was 258 mm. This is much longer and older than rivers farther south. Leaf River smolts may be the largest natural smolts produced. Estimated lengths at migration of smolts from other Ungava rivers were: 215 mm, George River; 206 mm, Whale and Koksoak rivers (Power 1969). Large smolt size may increase survival at sea (Lindroth 1965) and act as a compensatory mechanism to offset what must be a low production per unit area of smolts in the Ungava rivers.

Many juvenile male fish become sexually mature in Leaf River but no precocious females were observed with gonads in a sufficiently advanced state of development to indicate they would have spawned that autumn. Sexual maturity among the males has two effects. It occurs at the expense of growth (Fig. 2) and this explains the consistently smaller average size of males in all age-groups of juvenile fish beyond 2 (Table 1). It involves either a higher mortality rate, or it inhibits downstream dispersal with a tendency to eliminate the marine phase of the life cycle. Sex ratios (Tables 1–3) are weighed heavily in favor of females. For smolts (Table 3) the ratio was 5:1 in favor of females; for adults it was 3:1. These ratios are similar to those reported for other Ungava rivers by Power (1969) except that the shortage of male smolts is even more pronounced. Presumably on the spawning grounds the sex ratios are balanced by the participation of precocious nonmigratory males in the spawning act.

Upstream migration of mature adult salmon occurs in August and early September, at the same time as in the other Ungava rivers. A period of neap tides between August 14 and 18 coincided with peak landings in the 1968 Koksoak River fishery, where landings continued to be good until about August 25. This agrees exactly with the pattern of catches for the small sample of fresh-run salmon taken in the Leaf River. The sizes and weights of adult salmon entering Leaf River were within the range of sizes and weights of salmon entering other Ungava rivers to spawn.

A question is raised about the long-term viability of the Leaf River stock of salmon. It is apparently not large and it exhibits a life cycle which, in common with that of the salmon of the Kapisigdlit River in West Greenland (Nielsen 1961), has gone a long way towards elimination of the marine phase of the life cycle for at least part of the population. Dunbar (1972) suggested that the present marine distribution of salmon may be the result of a warming trend in the waters off West Greenland that began about 1915 and has subsequently reversed. Feeding salmon are concentrated in northwest Atlantic waters at temperatures between 3 and 8 C and few are captured in water below 2 C (May 1973). At the meeting of the Program Working Party on Atlantic Anadromous Fish, Quebec City, 1975, Mr H. Lear in discussing the late start of the 1974 commercial salmon fishery in Labrador and Newfoundland made the point that salmon seem to avoid sea temperatures below 2 C. The season of sufficiently warm sea temperatures is critically short in Ungava Bay and further cooling could conceivably eliminate anadromous salmon from the region. Under these circumstances there is good reason to suppose that Atlantic salmon would continue to inhabit the rivers, completing their entire life cycle in fresh water and perhaps the estuaries that would be warmer than the sea. The salmon reported from the Kugaluk River by Le Jeune and Legendre (1968) are almost certainly relicts from a former period of warmer climate. Other relict populations may await discovery in northern Quebec.

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Outbreak of Infectious Pancreatic Necrosis in Yearling Brook Trout (*Salvelinus fontinalis*)

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Studies were conducted to determine the etiology of an epizootic disease occurring in fry and yearling brook trout (*Salvelinus fontinalis*); clinical signs, experimental infection, and pathological lesions suggested infectious pancreatic necrosis. Electron microscopy and physicochemical characteristics were used to identify the virus isolated from sick trout as IPN virus. The isolates showed only partial antigenic similarity to the reference strain IPN VR_{299}. Increased susceptibility to IPN virus was observed in one genetic line of trout.

ELAZHARY, M. A. S. Y., A. LAGACE, G. COUSINEAU, R. S. ROY, L. BERTHIAUME, P. PAULHUS, AND J. L. FRECHETTE. 1976. Outbreak of infectious pancreatic necrosis in yearling brook trout (*Salvelinus fontinalis*). J. Fish Res. Board Can. 33: 2621–2625.

Cette étude a été entreprise dans le but de déterminer l'étiologie d'une condition épizootique se produisant chez des truites (*Salvelinus fontinalis*) âgées d'un an et les alevins. Les symptômes, l'infection expérimentale et les lésions pathologiques suggèrent comme cause de cette infection, la pancréatite nécrotique infectieuse. La microscopie électronique et les caractères physico-chimiques ont été utilisés pour identifier le virus isolé des truites malades comme étant le virus de la pancréatite nécrotique infectieuse. Le virus isolé possède une ressemblance antigénique partielle avec la souche de référence VR_{299} de la pancréatite infectieuse (IPN). Une susceptibilité accrue au virus IPN fut observée chez une lignée de truite.

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THIS note represents, to our knowledge, the first report of an outbreak of IPN in yearling brook trout (*Salvelinus fontinalis*), although Yamamoto (1973) reported the isolation of IPN virus from the kidney of clinically normal yearling trout.

Infectious pancreatic necrosis (IPN) is a viral disease that affects many species of salmonids: brook trout (Wolf et al. 1960), cutthroat trout (*Salmo clarki*) (Parisot et al. 1963), brown trout (*S. trutta*) (Wolf 1964), and coho salmon (*Oncorhynchus kisutch*) (Wolf and Pettijohn 1970).

IPN outbreaks in fry and fingerling trout populations have been reported in the U.S. (Wolf et al. 1960), Canada (Mackelvie and Artsob 1969), Japan (Sano 1971a, b), France (Besse and de Kinkelin 1965), Denmark (Jorgensen et al. 1969), and Scotland (Ball et al. 1971). These outbreaks were characterized by rapid onset and high mortality in fry and fingerling trout.

Effect of age on susceptibility of trout to this viral agent has been studied by Frantsi (1972) who found that the susceptibility of young brook trout to IPN virus decreases with increasing age. At 6 mo the trout became resistant to this viral agent (Frantsi 1972).

Materials and methods — Two genetic lines of brook trout (*S. fontinalis*) imported from a hatchery known to be free of IPN for 3 yr were raised in the same hatchery but kept separately. The hatchery was completely new; no other fish have been raised there before. Type A included fry (0+) and yearling trout (1+), while type B trout were yearlings (1+). Water was supplied to the different pools from a natural lake at a rate of 436,000 liters/min. Each pool received its water individually from the same source without recirculation between them.

Clinical observations were made by regular inspection in the trout hatchery and all mortalities were reported immediately.

Necropsy and histological examination were conducted in sick and dead trout. All external and internal organs were examined for macroscopic lesions. Histological examinations were made of fish that died during the natural outbreak, and of experimentally infected fish. After 24 h of fixation in 10% formalin, tissues were embedded in paraffin, sectioned at 6.0 μ, and stained with hematoxylin, phloxin, and safranine.

Virological examinations were carried out using the RTG-2 cell line. The cells were routinely cultivated at 18 C in Eagle's minimum essential medium (MEM) supplemented with 5% fetal calf serum, 100 IU/ml penicillin, 100 mg/ml streptomycin, and 0.25 μg/ml fungizone.

Samples were collected and processed as follows. The visceral organs from every three moribund brook trout were pooled, homogenized (Omnimixer Sorval, Ivan Sorval, Inc., Norwalk, Connecticut), and prepared as a 4% final suspension in Hank's balanced salt solution (pH 7.1–7.8). The suspensions were centrifuged at 650 *g* for 15 min and the supernatant was filtered through 0.22-mμ Millipore filters (Millipore Corporation Ltd., Bedford Massachusetts).

For each filtrate three tubes of RTG-2 cells (in which the monolayers were 70% confluent) were inoculated with 0.1 ml of filtrate and incubated at 18 C for 10 days. The cultures were examined periodically to check for cytopathic effects (CPE) and if none were recorded, three tubes of RTG-2 cells were inoculated for a second passage.

Virus titration from tissue homogenates was performed according to Hsiung (1973) by diluting in Eagle's MEM and using at least four cell culture tubes per virus dilution. Fifty percent end points were calculated by the method of Reed and Muench (1938).

To identify the isolate the following criteria were analyzed. The viruses were examined for resistance to ethyl ether and glycerol according to Hsiung (1973) at 18 C. Virus replication in RTG-2 cells at 10 and 21 C was also studied. Two basic neutralization tests were conducted in cell culture using goat antiserum (Microbial Associates, Inc., Bethesda, Maryland) against strain VR_{299} (American Type Culture Collection, Rockville, Maryland) of IPN virus. In the first neutralization test, serial tenfold dilutions of virus were mixed in equal volumes with IPN antiserum diluted 1:100. In the second test, twofold dilutions of antiserum (IPN) were reacted with a constant quantity of virus (100 median cell culture infectious dose [$CCID_{50}$] per 0.1 ml). In both tests the virus and serum mixtures were incubated at 18 C for 60 min before inoculation into cell culture. Then, 0.2 ml of each dilution was inoculated into each of three RTG-2 tubes cultures. Normal goat serum was used as a control. All sera were inactivated at 56 C for 30 min before being used.

Electron microscopic studies were carried out using negatively stained preparations (Doane et al. 1969; Pavilanis et al. 1971) examined with a Philips 200 electron microscope.

Fish infectivity tests were also performed. One hundred 10-wk-old brook trout obtained from a hatchery known to be free of IPN were used for infectivity tests with the virus that we isolated from the outbreak in yearlings. The fish were divided into two groups of 50. The first group was exposed to our IPN strain isolated from yearling trout of Type A whereas the second group was kept as a control. Daily clinical observations were carried out for 30 days.

The heads from diseased fish were examined for the presence of *Myxosoma cerebralis* according to the method of Hoffman et al. (1962). Diseased trout were routinely examined for bacteria and parasites.

Results — Clinical observations — Uncoordinated movements and spiral swimming were the clinical signs observed during the outbreak in yearling brook trout of Type A. Ten days later

fry of type A showed the same signs. Seven percent of the yearlings had died by day 11 while 27% of the fry had died by day 25.

Yearling brook trout of type B did not die or manifest clinical signs of IPN before, during, or after this outbreak in type A trout.

Pathology — In fry, the stomachs and intestines were distended by a clear mucous material and contained no food. In yearling trout, only the intestines were distended.

Advanced lesions were seen in the pancreas of both yearlings and fry. Sometimes, only a few pancreatic cells could be recognized, while pyknotic nuclei, cellular debris, secretion granules, a few inflammatory cells, erythrocytes, and amorphous material replaced the pancreatic tissue (Fig. 1). Normal pancreatic tissue of yearling trout is seen in Fig. 2.

In other fish, the lesions were more localized and surrounded by normal-looking pancreatic tissue. Both acinar and islet tissue were occasionally necrotic. A few cyptoplasmic bluish inclusion bodies were seen in one less severely affected fish.

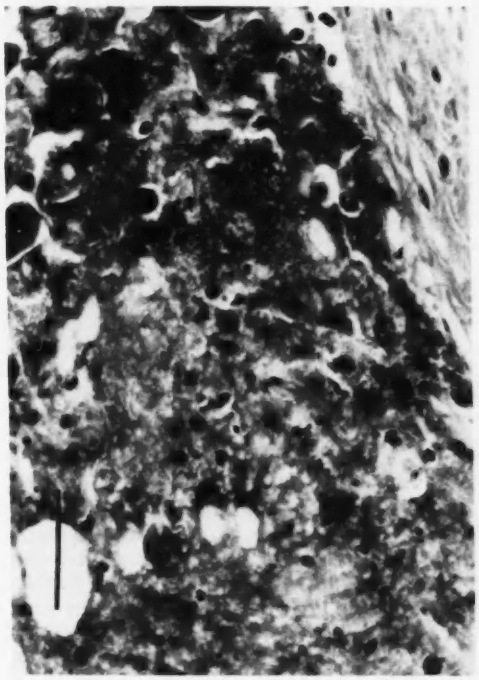

FIG. 1. Pancreas of a yearling (1+) brook trout (*Salvelinus fontinalis*). Only a few pancreatic cells can be recognized. Pyknotic nuclei, cellular debris, secretion granules, inflammatory cells, and amorphous material replace the pancreatic tissue. Fixed sections stained with hematoxylin, phloxin, and safranine. Bar represents 100 mμ.

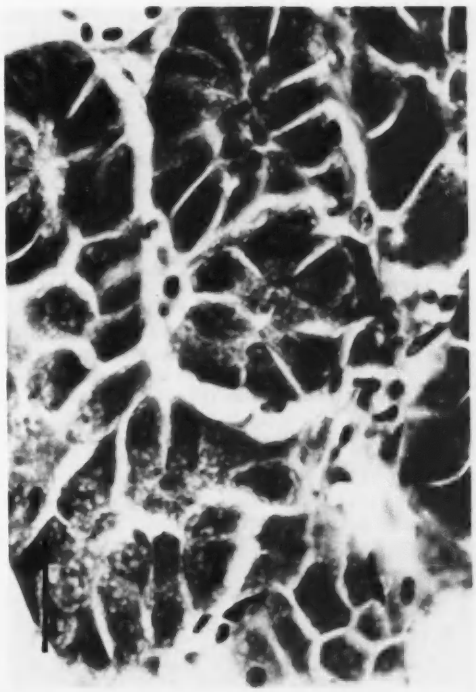

FIG. 2. Normal pancreas of a yearling (1+) brook trout. Fixed section stained with hematoxylin, phloxin, and safranine. Bar represents 100 mμ.

No significant kidney lesions were found and hyaline degeneration of skeletal muscle, while seen in some diseased fish, was also present in some of the control fish of the same ages. The examination of tissue for *M. cerebralis* gave negative results.

Virology — The visceral homogenates from type A yearlings and fry had a viral titer of $10^{4.3}$ and $10^{3.2}$ $CCID_{50}$/ml, respectively. The two viruses were stable after a 2-h treatment with 10% ethyl ether and 2- and 24-h exposures to 50% glycerin. Both viruses produced CPE at 10 and 21 C as well or better than at 18 C.

The neutralizing capacity of VR_{299} antiserum for the two isolated viruses was consistently lower than for the reference strain (Table 1). There was partial serological identity between our isolates and the reference strain (Table 2).

Negatively stained preparations of the two

TABLE 1. Comparative neutralization indices of two Quebec isolates and VR_{299} virus using antiserum against reference strain VR_{299}.

Virus strain	Titer expressed as exponent of $\log_{10}$ infectivity (50% end point) per ml		
	virus + normal serum	virus + VR_{299} antiserum	neutralization index
VR_{299}	6.5	1.2	5.3
From yearling trout	5.4	4.3	1.1
From fry trout	6.2	5.4	0.8

TABLE 2. Comparative neutralization test of the two Quebec isolates and reference strain VR_{299} virus.

Serum	VR_{299} 100 $CCID_{50}$	From yearling trout 100 $CCID_{50}$	From fry trout 100 $CCID_{50}$
Normal	<1:4	<1:4	<1:8
Anti VR_{299}	1:3856	1:64	1:32

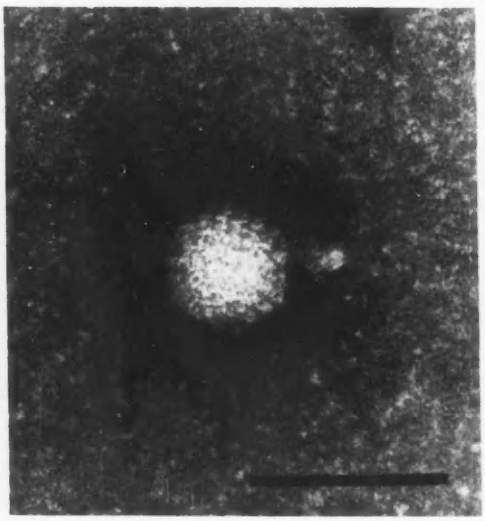

FIG. 3. Negative stain (PTA) of IPN virus particle. Four capsomeres can be seen on an edge (arrows) of the capsid. 300,000×. Bar represents 100 nm.

viruses (Fig. 3) showed hexagonal virus particles, approximately 60 nm diam from edge to edge or 70 nm from apex to apex. Capsomeres on the capsid surface were visible, and four capsomeres were seen on some capsid edges. Observations suggest that this virus was made of 92 capsomeres. Empty particles never revealed the characteristic inner capsid of the reoviruses.

Experimental infection of 10-wk-old trout was made using our viral isolate from yearlings. Twisting motion which consisted of rotating about the long axis was common among experimentally infected trout fry. Mortality began on the 7th day after infection and rose sharply between days 7 and 8. By day 9, 60% of the fish were dead.

Discussion — During the epizootic of the disease and in fish infectivity trials the diseased trout showed clinical signs and pathological lesions similar to those of IPN as described by Mackelvie and Artsob (1969) and Wood et al. (1954).

We identified the isolated viruses as reo-like viruses (Kelly and Loh 1972) by their lack of an inner capsid, their poorly defined capsomeres, and their shape and size. They were similar in these respects to IPN virus (Moss and Gravell 1969).

The poor reactivity of these viruses with VR_{299} antisera indicated that our two strains are distinct from this reference strain. Serological diversity of IPN viruses has been reported in North America (Malsberger and Cerini 1963; Mackelvie and Artson 1969) and in Europe (Jorgensen and Kehlet 1971). Moreover, Wolf and Quimby (1971) reported that IPN viruses isolated from trout from France are antigenically distinctive from the VR_{299} strain.

The stability of the two isolates in the presence of ether and glycerin and their replication at 10 and 21 C differentiate them from EGTVED and infectious hematopoietic necrosis virus (Jorgensen et al. 1969; Holway and Smith 1973). Considering the above mentioned data, IPN virus is re-

garded as the etiological agent of the epizootic disease reported among yearling trout.

Variation in resistance of certain genetic lines of fish to *Pseudomonas* and *Escherichia* has been reported by Gontcharov and Mikriakov (1968). Similar patterns in susceptibility could be suspected in yearling trout since these two groups of trout originated from different lines. The susceptibility in trout from different genetic origin to IPN virus will be studied in the future.

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Coded Spine Clipping to Identify Individuals of the Spiny-Rayed Fish *Tilapia*

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RINNE, J. N. 1976. Coded spine clipping to identify individuals of the spiny-rayed fish *Tilapia*. J. Fish. Res. Board Can. 33: 2626–2629.

Clipping 1 or more spines in the dorsal and anal fins was used to identify individual *Tilapia*. In fish > 15 cm the mark was permanent. In smaller fish spine regeneration occurred, but clipped spines could be recognized both by their incomplete regrowth and abnormal appearance. This technique is applicable not only to experimental situations requiring recognition of individuals but also to group marking and to other Perciforms.

RINNE, J. N. 1976. Coded spine clipping to identify individuals of the spiny-rayed fish *Tilapia*. J. Fish. Res. Board Can. 33: 2626–2629.

Le sectionnement d'une ou de plusieurs épines des nageoires dorsale et anale a servi à identifier des *Tilapia* individuels. Chez les poissons plus grands que 15 cm, la marque est permanente. Chez les poissons plus petits, il y a régénération, mais l'apparence anormale des épines sectionnées permet de les distinguer des épines non sectionnées. Cette méthode de marquage est applicable non seulement aux expériences où il est nécessaire de reconnaître les individus, mais aussi à des marquages en groupe de cette espèce et d'autres perciformes.

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IN growth and tagging experiments on several species of *Tilapia* that inhabit Lake Victoria, East Africa (Rinne 1975), it became necessary to recognize test fish to 1) control frequent contamination of research ponds and aquaria with nonexperimental animals, 2) follow individual fish through maturity, and 3) define growth differential between sexes. Stott (1971) has recently listed and discussed conventional methods of marking and tagging. However, these were not applicable to my study due to small size of experimental animals, availability of materials, and the probable effect on behavior and growth of fishes.

Van Sommern and Whitehead (1959) employed the soft rays of the pelvic fins in batch (group) marking of *Tilapia* under tropical conditions. In addition to the soft fin rays *Tilapia* contain true spines in the dorsal and anal fins. I developed a coded method of clipping dorsal and anal spines to identify fishes for experimentation. This note describes the procedure of coding, mark retention, identification, and spine regeneration.

Materials and methods — Growth experiments for *Tilapia* were conducted on or near Lake Victoria at Kisumu, Kenya. Methodology developed and data presented were acquired secondarily to the primary objective of growth estimation. Therefore, sample size, time periods, and animals marked were dictated by this research program. As a result, varying numbers of *T. nilotica*, *T. zillii*, and *T. variabilis* were spine-clipped and placed into aquaria and ponds. Also, fishes were often coded in sequence and it was not possible to place equal emphasis on either a species or spine basis. Specimens were examined and mean growth rates of fishes and percent regeneration of spines were estimated only at the termination of each growth experiment. Time periods varied from 4 to 6 wk.

The three species of *Tilapia* I studied have 14–18 spines in the dorsal fin and 3 in the anal. Interspine tissue is incised with small surgical scissors and spines are clipped at the extreme proximal end. The 1st 9 dorsal spines are coded as units; the 10th to the last as tens (Fig. 1A). The 11th spine is designated as 20, the 12th as 30, etc. In turn, the anal spines are utilized as hundreds. Single spines are removed from fishes numbered 1 through 10 and multiples of 10 (e.g. 20, 40, 100). Other numbers involve clipping of 2 or more spines. For example, a fish numbered 14 has its 4th and 10th dorsal spines cut (Fig. 1B). One with the 7th and 10th dorsal spines clipped and the 1st anal would be 117.

The number of fish discernible in each species of *Tilapia* depends on mean number of dorsal and number of anal spines. *Tilapia variabilis* and *T. nilotica* have an average of 16 and 17 dorsal spines,

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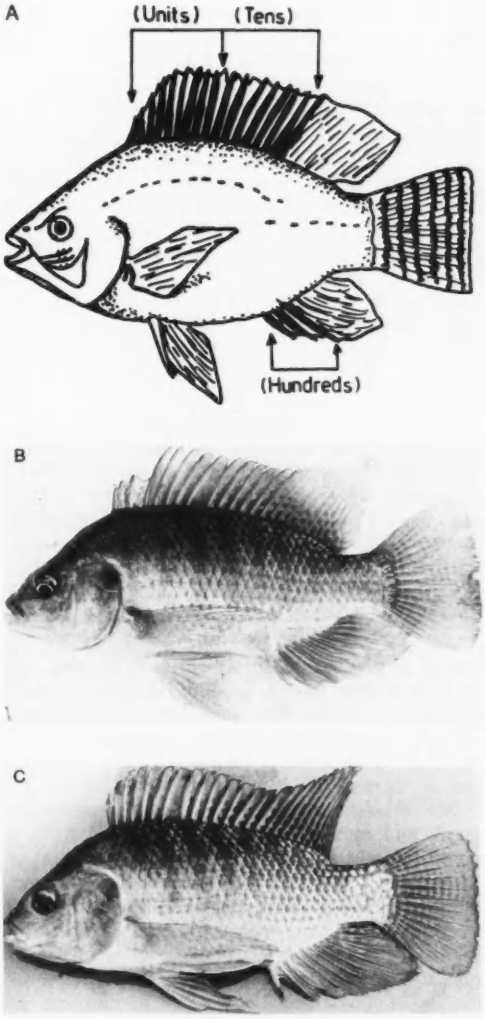

FIG. 1. A, Sketch of *Tilapia nilotica* indicating spine designation used in coding of individuals; B, C are samples of regeneration of spines of several individuals: B, no. 14 (20 cm TL) and C, no. 8 (21 cm TL).

respectively; this permits up to 79 individuals to be numbered in the former species and 89 in the latter. Total animals marked using the dorsal fin can be repeated 7 times by employing anal spines singularly and in combination (e.g. remove 1st and 2nd spine = 400s; 2nd and 3rd, 500s; 1st and 3rd, 600s; and all 3 anal spines, 700s). Therefore, approximately 640–720 individuals of these two species may be marked in a given research environment. Since *T. zillii* contains fewer dorsal spines (mean 15) fewer fish (560) can be marked in a single research environment. Numerical limits of this coding system listed for each species may be exceeded by utilizing groups of animals of markedly different lengths dependent upon respective research environment and design.

Preliminary observations on regeneration of spines — One experiment included 120 spine-clipped *T. nilotica* that grew from a mean total length (TL) of 8.8–11.7 cm in 4 wk (2.9 cm/mo). At termination 80 individuals (67%) could be discerned by respective spine clips. In another experiment of 2 mo, 20 *T. nilotica* (6.1 cm, mean TL) grew 4 cm/mo; fifteen fishes (75%) could be differentiated by spine clips. These individuals were reclipped and 2 mo later (17.9 cm, mean TL; 1.9 cm/mo) all animals were recognizable. The longest experiment (4 mo) utilized *T. nilotica* 5.5 cm in mean TL that grew to 18.8 cm (3.3 cm/mo). Only 7 of 20 individuals (35%) could be positively distinguished. Of these, 4 showed no regeneration of clipped dorsal spines, and 1 each displayed 50, 75, and 100% estimated regrowth. The abnormal appearance of the 1 fully regenerated spine suggested that through careful observation and training even these spines could be detected.

Results of detailed studies on regeneration of spines — Dorsal spines of *T. zillii* which grew an average of 0.2 cm/mo in aquaria were usually less than 50% regenerated (Table 1). By comparison, most (84%) fish that grew between 1.5 and 5.9 cm/mo in ponds also showed 50% or less regeneration of dorsal spines. In agreement with data for dorsal spines, anal spines regenerated to only half or less their former size in either aquaria or ponds.

Tilapia nilotica that were reared in aquaria and grew at a rate similar to *T. zillii* regenerated spines more rapidly. Regrowth of dorsal spines was somewhat slower in the largest size-group (12.5 cm TL). More rapid growth rate of fish and regrowth of spines occurred in ponds. However, no direct relation between size and growth rate of fish and regeneration of spines was evident. Anal spines were regenerated in similar fashion to dorsals.

Most (68%) *T. variabilis* that were held in ponds and grew about 2 cm/mo displayed 50–75% estimated regeneration of dorsal spines (Table 1). Only 2 of 44 (5%) showed complete regrowth of clipped spines. These can be recognized by their curved and thickened appearance.

Experiments conducted in aquaria indicated both slower growth of fishes and regeneration of spines. Based upon relative percentages, regrowth of spines was most rapid in pond-reared *T. variabilis* followed by *T. nilotica* and *T. zillii*, respectively.

Because population densities, time intervals, and initial size of fish in respective experiments

TABLE 1. Regeneration rates (percent) of dorsal and anal spines of *Tilapia* spp. reared in aquaria and ponds.

n	Initial mean total length (cm)	Mean monthly growth rate (cm)	Exp time (wk)	% regeneration									
				Dorsal spines					Anal spines				
				0	25	50	75	100	0	25	50	75	100
			Aquaria										
Tilapia zillii													
49	7.6 (6.8–8.8)	0.3 (0.1–0.6)	4	10	33	43	14	0	6	44	38	12	0
16	11.8 (11.5–12.1)	0.1 (0.0–0.2)	4	50	19	31	0	0	88	12	0	0	0
T. nilotica													
27	7.1 (7.1–7.2)	0.1 (0.0–0.2)	5	26	11	33	30	0	8	14	56	22	0
72	10.6 (9.9–10.9)	0.2 (0.0–0.6)	5	57	6	13	22	2	50	18	24	8	0
48	12.5 (11.4–13.5)	0.1 (0.0–0.2)	4	71	3	13	13	0	25	25	8	27	15
			Ponds										
T. zillii													
87	8.4 (6.3–9.3)	3.6 (2.6–5.9)	6	23	19	25	28	5	16	40	40	4	0
5	14.3 (12.6–15.1)	1.6 (1.5–1.7)	6	80	20	0	0	0	—	—	—	—	—
T. nilotica													
23	7.3 (6.8–7.3)	5.6 (5.7–5.9)	6	39	4	13	22	22	0	9	22	26	43
18	11.3 (10.9–11.7)	2.0 (1.5–2.5)	6	39	17	0	0	44	—	—	—	—	—
T. variabilis													
44	8.1 (7.2–9.0)	2.1 (1.8–2.3)	4	16	11	20	48	5	—	—	—	—	—

were dictated by the primary objective of growth estimation and because these factors would obviously affect growth of fishes and perhaps regeneration of spines, specific growth (percent change in growth per day) rates were calculated:

$$\text{Sp growth} = \frac{\log l_2 - \log l_1 \times 100}{\text{days}}$$

where: l_2 = final length of fish and l_1 = initial length of fish. These values were then compared by linear regression to the percentage of fish in each experiment with 50% of their dorsal spines regenerated. Correlation coefficients (r) for comparison of fishes reared in ponds ($r = 0.51$), aquaria ($r = 0.115$), and the combination of all experiments in the two environments ($r = 0.230$) were nonsignificant ($P > 0.05$).

Discussion — Although rapid tissue regeneration of fin-clipped *Tilapia* in the tropics has been recorded (Van Sommern and Whitehead 1959), the spine-clipping technique is effective for at least a month in small (<12 cm TL) fishes. Less than 50% regeneration normally occurs in both dorsal and anal spines and completely regenerated spines can be discerned. Similar observations were made by Van Sommern and Whitehead (1959) for the soft pelvic fin-rays of *T. nigra*.

Spines were regenerated more rapidly on fish reared in ponds than those reared in aquaria and in *T. variabilis* and *T. nilotica* than in *T. zillii*. Apparent increased duration of marks in artificial aquaria environments and the capability of reclipping potentially increases the design of research intervals.

Notwithstanding extremes recorded between ponds and aquaria, there does not appear to be a consistent, direct relation in rate of growth of *Tilapia* and regrowth of spines. For example, although relative spine regeneration in the two size-groups of pond-reared *T. zillii* fit this hypothesis, it fails to hold for *T. nilotica* grown in ponds. This is somewhat paradoxical in view of the well-documented body–scale relationship in fishes which presumably is controlled by the same calcifying mechanisms. Nevertheless, the lack of significance of r-values calculated from comparison of specific growth rates (which remove the variables of population density, size of fish, and time intervals) and the percentage of fish with 50% or more regeneration of spines supports this suggestion.

Large fish (>12 cm), however, do display less rapid regeneration of spines as they approach the peak of their asymptotic growth curve. Specimens of both *T. nilotica* and *T. zillii* >15 cm have greatly reduced to no regrowth of spines (Fig. 1C). To insure identification, smaller fish (7–10 cm) may be reclipped at monthly intervals until

>15 cm long. Mortality in the size range of fishes examined is low to nonexistent and on the basis of data in Rinne (1975) spine clipping did not reduce the growth rate of *Tilapia*.

This marking technique permits labeling of between 560 and 720 individuals in a given size-group or species of *Tilapia* that I studied. It could also be employed in group markings and thereby allow designation of an infinite number of fish. In other cichlids in East (e.g. *T. nigra*) and South Africa (*T. placida*) (Trewavas 1966) and in North and Central America (*Cichlasoma*) that have more than 3 anal spines, even more individuals could be spine-coded. Also, this method may be readily applied to other fishes in the families Percidae and Centrarchidae; however, to increase sample size, soft rays in the dorsal fin could be employed in those species with 10 or fewer dorsal spines.

Both basic and applied experiments and commercial enterprises could employ this system of marking. In addition to growth studies, it has been successfully utilized for identification of individuals of *T. nilotica* and *T. zillii* in preliminary pesticide experimentation in aquaria. It has the advantage over other methods of marking of reduced effect on fish growth, mortality, behavior, and general well being. Further, it is a natural device and is economical. Initially, mating behavior and related fin movements may be affected. No direct observations into this problem were made in this study, but based on spawning products of marked fishes observed in ponds this influence apparently ceases with regrowth of interspine tissue.

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Effects of Air-Supersaturated Water on Adult Sockeye Salmon (*Oncorhynchus nerka*)

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Adult sockeye salmon (*Oncorhynchus nerka*) were exposed to air-supersaturated water in the laboratory from July 8 to August 13, 1974, approximately the same time period that they are exposed to supersaturated water during their movement through the lower and middle sections of the Columbia River. The first mortality occurred after 77 h exposure at 120% saturation; 40% of the fish were dead after 127 h. At 115% saturation the first mortality occurred after 523 h (21 days) and 40% were dead after 835 h (35 days). No further mortality occurred at 120 or 115%. However, at 120 and 115% saturation, survivors exhibited many sublethal lesions such as hemorrhaging and emphysema (bubbles) in the mouth, on the gill arches, body surface, and fins, etc. No deaths or signs of gas bubble disease occurred in fish held at 110% saturation in water 2 ft (60 cm) deep. The lethal threshold was near 114% saturation.

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Des saumons nerka (*Oncorhynchus nerka*) adultes ont été exposés à de l'eau sursaturée d'air en laboratoire du 8 juillet au 13 août 1974, soit pendant à peu près la même période où ils sont exposés à de l'eau sursaturée lors de leur passage dans les cours inférieur et moyen du fleuve Columbia. Les premières mortalités se produisirent après exposition de 77 h à une saturation de 120%; 40% des poissons étaient morts après 127 h. A une saturation de 115%, les premières mortalités se produisirent après 523 h (21 jours) et 40% des poissons étaient morts après 835 h (35 jours). Il ne se produisit pas d'autres mortalités à 120 ou à 115%. Cependant, à des saturations de 120 et de 115%, les survivants montrèrent plusieurs lésions sublétales telles qu'hémorragies et emphysème (bulles) dans la bouche, sur les arcs branchiaux, la surface du corps et les nageoires, etc. Il n'y eut pas de mortalités ni de signes de maladie de bulles gazeuses chez des poissons maintenus à une saturation de 110% dans une profondeur d'eau de 2 pi (60 cm). Le seuil létal est dans le voisinage de 114% de saturation.

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ADULT Pacific salmon become afflicted with gas bubble disease (GBD) caused by air-supersaturated water in the Columbia River. The supersaturated water, routinely found up to 130–140% total air saturation, is created by air entrained in the water as it spills over the hydroelectic dams on the river. The severity of the GBD problem has been noted (Rucker 1972; Ebel 1969; Westgard 1964), but it is difficult to document and quantify in the river because of the many other factors affecting fish survival during the upstream spawning run.

In an attempt to determine the impact of GBD, tests were conducted at the Western Fish Toxicology Station (WFTS–EPA), Corvallis, Oreg. There, under controlled conditions, certain variables could be eliminated to isolate gas supersaturation from other stresses found in the Columbia River. Bouck et al. (1976) presented data on acute lethality of gas-supersaturated water to adult sockeye (*Oncorhynchus nerka*), coho (*O. kisutch*), and chinook (*O. tshawytscha*) salmon. This note presents additional information dealing with the longer-term effects of supersaturated water on adult sockeye.

Materials and methods — Adult sockeye were collected from the supersaturated Columbia River at the Bonneville Dam north fish ladder and transported to WFTS in a refrigerated tank truck. They were placed in a holding tank, then randomly selected and transferred to four, circular, 3.6 m diam test tanks that had a water depth of 60 cm and held 6000 liters of water. Ten fish were placed in each tank and held at 13–15 C for 1 wk before the test water was supersaturated. Test facilities and supersaturation generators used are described in Nebeker et al. (1976). Water was supersaturated by injecting compressed air into the water supply system under pressure and then releasing the test water to the tanks under normal atmospheric pressure. The saturation (percent) was controlled by the amount of air injected into the test water.

The fish were tested at total dissolved gas saturation levels of 120, 115, 110, and 100% at 12 C. The test duration was 35 days, spanning the 2–3-wk time period the salmon would be expected to be exposed to gas-supersaturated water in the Columbia River. Water velocity in the circular tanks was maintained at 10–15 cm/s, with a flow rate through the tanks of 40 liters/min. Saturation levels were measured with the Weiss saturometer (Nebeker et al. 1976) using the formula: $\frac{BP + \Delta P - VP}{BP} \times 100 = \%$ saturation, where BP = barometric pressure, ΔP = saturometer reading, and VP = water vapor pressure (Table 1). Chemical analyses of the test water are reported in Samuelson (1976).

Examination of the fish for lesions and signs of gas bubble disease followed the methods outlined by Stroud et al. (1975). Necropsy examinations were conducted on 14 of the 40 test fish to determine cause of death and extent of supersaturation-induced lesions. The threshold concentration (that concentration where significant mortality no longer occurs) was determined using methods similar to those of Sprague (1969).

Results and discussion — Saturation levels of 120 and 115% caused mortality and extensive sublethal signs of GBD in the sockeye; however, fish held at 110% did not appear to differ in behavior or survival from the control salmon at 100% saturation. At 120% saturation, the first fish died after 77 h exposure. The second and third fish died at 100 and 115 h, respectively. At 127 h, the fourth (and last) fish died at 120% saturation (Table 2). Gross lesions of bacterial or fungal infections were not noted during the test in fish held at 120%. Survivors remained near the bottom of the tank, swimming quietly unless disturbed.

TABLE 1. Nominal and measured test levels of total gas supersaturation.

Test tank[a]	Nominal total gas saturation (%)	Measured total gas saturation[b] N	Mean ± *SD*	Range
1	120	63	119.8±0.63	118.1–121.7
2	115	44	115.4±1.45	113.0–119.5
3	110	60	109.5±0.82	106.3–110.7
4	100	—[c]	—[c]	—[c]

[a]6000-liter tank.
[b]Analysis with Weiss saturometer.
[c]Remained near 100% at all times.

TABLE 2. Mortality of adult sockeye salmon (*Oncorhynchus nerka*) tested at 120, 115, 110, and 100% total dissolved gas supersaturation at 12 C.

Nominal % super-saturation[a]	Fish no.	Time to death (*h*)	Sex	Weight (*kg*)	Length (*cm*)
		Tank 1			
120	1	77	F	1.6	52
	2	100	F	1.7	53
	3	115	M	1.8	53
	4	127	M	1.9	54
	5	—[b]	F	1.4	53
	6	—[b]	M	1.7	54
	7	—[b]	M	2.0	57
	8	—[b]	—[c]	1.9	58
	9	—[b]	M	1.6	53
	10	—[b]	—[c]	1.7	54
		Tank 2			
115	1	523	M	2.3	59
	2	667	F	1.7	52
	3	835	—[c]	1.5	54
	4	835	—[c]	1.7	56
	5	—[b]	M	0.5	39
	6	—[b]	—[c]	1.4	53
	7	—[b]	—[c]	1.4	51
	8	—[b]	M	0.8	42
	9	—[b]	—[c]	—[c]	—[c]
	10	—[b]	—[c]	—[c]	—[c]
		Tank 3			
110	1–10	—[b]	No observed GBD		
		Tank 4			
100 (Control)	1–10	—[b]	No observed GBD		

[a]Water depth of 60 cm.
[b]Alive after 30 days.
[c]Not determined.

All fish held at 120% were necropsied at death or at the end of the test to determine cause of death or to characterize the sublethal signs of gas bubble disease that had developed. In the first fish to die, subdermal emphysema (gas blisters) was present in the mouth (Fig. 1), in the dorsal, pectoral, and pelvic fins, and on the margin of the right opercle. The gills appeared congested and swollen, and were covered with excess mucus. When the gill arches were cut, blood and gas bubbled forcefully from the branchial arteries indicating that gas emboli were present under significant pressure in the blood stream flowing to the gills. Gas emboli filled the bulbus arteriosus and ventral aorta, and emboli could be seen in the coronary arteries. Gas emboli were observed in the blood vessels supplying the retina of the eye, and blood, presumably from the rupture of these distended vessels, was present in the left eye.

The second fish to die at 120% (100 h) had bubbles in the scale pockets and on top of individual scales. Gas blisters up to 2 cm diam were observed on the body, and hemorrhages were associated with the gas blisters along the sides of the body (Fig. 2). The pectoral, pelvic, and caudal fins contained gas blisters and hemorrhages, and gas blisters occurred on the inside of the gill covers. The gills were cyanotic and covered with mucus, and blood from cut gill arches contained many gas emboli. Blood vessels in the brain were congested, and gas emboli were observed in the coronary vessels. Emboli were pre-

FIG. 1. Adult sockeye salmon (*Oncorhynchus nerka*) with massive subcutaneous emphysema in the mouth and on the left opercle.

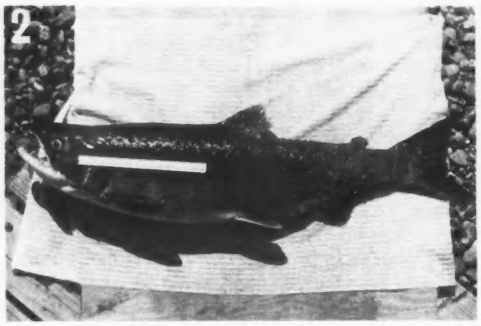

FIG. 2. Adult sockeye with subcutaneous emphysema scattered over the body and fins.

sent in the bulbus arteriosus, the ventricle and auricle, and free gas bubbles were observed in the kidney. Gas blisters were readily apparent under the skin at the base of the gill filaments and on the gill rakers (Fig. 3 and 4).

The third and fourth fish to die at 120% saturation exhibited similar lesions and apparently also died from massive blockage of blood flow in the heart, gills, and other capillary beds of the body. The six fish that did not die exhibited many GBD-caused lesions, but apparently did not suffer from massive emboli formation in the circulatory system sufficient to block blood flow to the gills and cause death.

The fish held at 115% saturation did not begin to die until later in the test; the first death occurred at 523 h. The fish exhibited many external lesions due to gas bubble disease, and bacterial and fungal infections became apparent in tissues devitalized by these lesions. On the first fish to die at 115%, gas blisters were observed on the roof of the mouth, the anal fin, the opercles, and at the bases of the gill arches. Fewer gas blisters occurred on the skin of fish tested at 115% than fish held at 120% saturation. The gills were discolored and the devitalized tissue heavily infected with fungus, giving them a matted yet soupy consistency. No emboli were observed in the heart or associated blood vessels. Gas blisters occurred on the pelvic and pectoral fins of the second fish to die at 115%. Fungal

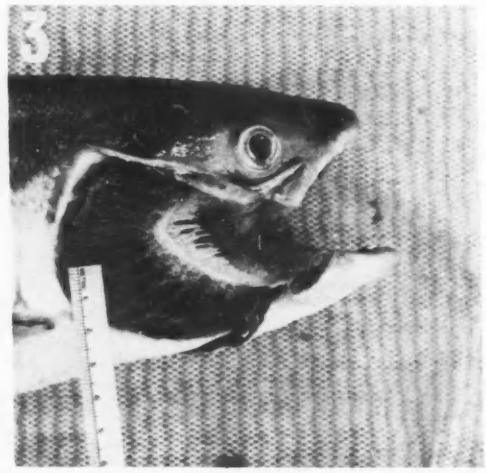

FIG. 3. Cutaway view of the head and gills of adult sockeye showing emphysema on gills, gill arches, and mouth cavity.

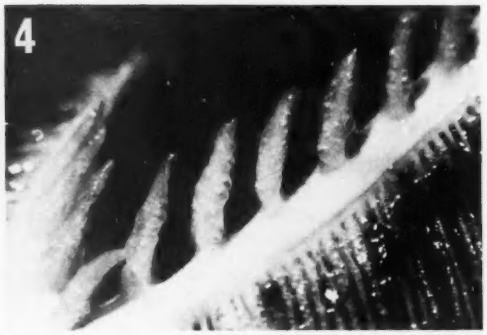

FIG. 4. Gill arch and rakers of adult chinook salmon (*O. tshawytscha*) showing massive subcutaneous emphysema (sockeye and chinook adults had similar gill arch pathology).

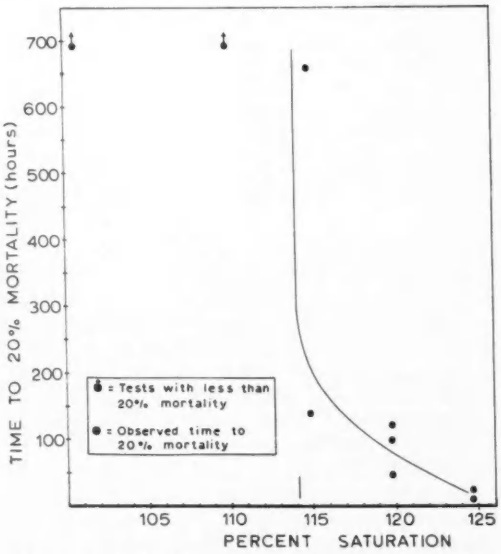

FIG. 5. Threshold concentration determined for adult sockeye (10 fish/test) at 12 C in 60 cm of water.

infections were severe on the body and fins and the right eye had been lost. The third and fourth fish to die at 115% saturation exhibited similar fungal lesions but no external emphysema was observed.

No lesions of gas bubble disease were observed in the fish held at 110% saturation and their behavior was similar to that of control fish.

The lethal threshold concentration (Fig. 5) determined for the adult sockeye at 12 C and 60 cm water depth was near 114%. Data from this study and earlier acute tests (A. V. Nebeker unpublished data) were used, and time to 20% mortality was plotted to obtain the curve. Based on these data, adult sockeye migrating through the Columbia River would probably not be affected by GBD if total gas saturation levels in the river remained below 115%. If the salmon were swimming in deeper water, the 10%/m (of water depth) reductions in total gas saturation due to increased water pressure would provide an additional safety factor.

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PERSPECTIVES

Aquatic Environmental Quality: Problems and Proposals[1]

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Abstract

HARVEY, H. H. 1976. Aquatic environmental quality: problems and proposals. J. Fish. Res. Board Can. 33: 2634–2670.

An overview was prepared of research and monitoring of aquatic environmental quality by federal and provincial agencies, the university, and private sectors. The overall effort in Canada was found to be unbalanced. Areas of strength were monitoring of water quantity, chemical water quality, and fish physiology–toxicology. Areas of weakness were the use of organisms and the use of whole systems as indicators of environmental quality. The amount of innovation was modest, due in part to the underutilization of the university community. In some areas of monitoring, data interpretation lags seriously behind data collection. A number of constraints now exist to our understanding of the source, distribution, and life expectancy of toxic substances in our environment, and these are discussed in relation to mercury. Specific problems of aquatic environmental quality are discussed by economic sector.

Résumé

HARVEY, H. H. 1976. Aquatic environmental quality: problems and proposals. J. Fish. Res. Board Can. 33: 2634–2670.

L'auteur présente une revue des travaux de recherche et de contrôle continu de la qualité de l'environnement aquatique effectués par les organismes fédéraux et provinciaux, les universités et le secteur privé. On se rend compte que, dans l'ensemble, l'effort canadien manque d'équilibre. Les points forts sont le contrôle de la quantité d'eau, de la qualité chimique de l'eau et de la physiologie–toxicologie des poissons. Les points faibles sont l'emploi d'organismes et de systèmes entiers comme indicateurs de qualité de l'environnement. Les innovations sont modestes en volume, à cause en partie de la sous-utilisation de la communauté universitaire. Dans certains domaines du contrôle continu, l'interprétation traîne loin derrière la cueillette des données. Il existe présentement plusieurs contraintes à notre compréhension de la source, de la répartition et de la durée des substances toxiques dans notre environnement, et l'auteur discute de ces points en relation avec le mercure. Des problèmes spécifiques de qualité de l'environnement aquatique sont examinés par secteur économique.

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Introduction

This study is one of a series commissioned by the Fisheries Research Board of Canada (FRB) in meeting its mandate to advise the Minister of State for Fisheries. The terms of reference were written by the Committee of the Board on Aquatic Environmental Quality, and accepted by the Board as a whole. The purpose of this study was to provide background information for the FRB Committee. This group had the responsibility of producing a succinct report for consideration by the Board and, thereafter, the Minister.

Terms of Reference

The study was divided between R. D. Hamilton and H. H. Harvey. The portion of the terms of reference falling to the latter author were:

Evaluate current Canadian monitoring programs on aquatic environmental parameters, placing emphasis on related programs as well as their individual and joint utility. Explore the practicality of using organisms and communities of organisms as indicators of water quality. Determine feasibility and desirability of federal support for research into the development of water quality indices and for the preparation of a water quality atlas.

Review and assess the relevance, emphases, adequacy, and effectiveness of the Fisheries and Marine Service research effort on aquatic environmental quality, in relation to the total Department of the Environment and national effort in this field. Particular attention should be given to the coordination of freshwater environmental quality research.

Scope of Study

Having used the phrase "aquatic environmental quality" it is obvious that this must be further defined in terms of "for what" or "for whom." In doing so, one is in effect listing the immense number of human activities and nonhuman processes that involve water. It would be simpler to try to identify those activities/processes that do not involve water. In the operational sense environmental quality is used as defined by Pimlott et al. (1971).

It is not surprising that many, often large institutions have been formed to deal with water. Nor is water the responsibility of any one level of government. Under the British North America Act of 1867, responsibility was shared between federal and provincial governments. Thus, eight federal departments are involved with water, and almost as many in each province. Boundaries

between provinces were seldom based on watersheds, and this requires interactions between provinces and the federal government on common waters.

Also, the international border passes midchannel through the Saint John, St. Lawrence, Rainy, and other rivers; through Memphremagog, Champlain, Ontario, Erie, Huron, Superior, St. Mary, Rainy, Lake of the Woods, and other lakes; the Red, Souris, Poplar, Milk, Kootenay, Columbia, Flathead, and other rivers cross the border one or more times. This requires yet another level of institutions to deal with water — international commissions.

By no means is all research on water done by these levels of government. The private sector, both that of industrial firms and of consultants, is appreciable and increasing rapidly. Historically, universities made a large contribution to research on many aspects of water. Finally, some provincial research councils have active research programs on water-based problems.

The challenge then was to assess this diverse, overall research effort and to attempt to categorize it into some manageable units. Hopefully this would make clearer some areas of overlap, of duplication of effort, of inadequate effort, and the problems that have remained nobody's responsibility.

This was not intended as a review article for scientists on the state of the science. This was written as a background document for an overview of government policy in relation to aquatic environmental quality, for the Fisheries Research Board of Canada. This Board intercepts the line-operation at the level of the Minister, that is, the Board advises the Minister of State for Fisheries on matters of policy.

Interpretation and Criteria

One term of reference of this study called for review and assessment of the relevance, emphases, adequacy, and effectiveness of the research effort on aquatic environmental quality. How does one measure things such as relevance, especially in view of the rapidly changing value-judgments in the area of environmental concerns? One approach is to assess these in terms of man-years expended and dollars spent for each category of environmental problem. That is, the measurement is that of effort expended without assessing its effectiveness. Such statistics are available for operational units within governmental agencies, but not by specific environmental problems. Thus, it is easy to identify the budget and personnel of, for example, a toxicology unit in a research station, but it is very difficult to identify the total effort in Canada on environmental problems or its effectiveness related to cadmium, for example.

An alternate approach is that taken by the Economic Council of Canada (ECC) and Science Council. Relevance and adequacy of government action is measured not on the basis of expenditures made, but on results achieved. Thus, for example the ECC does not advise the federal government on how to juggle its financial and personnel resources, but rather assesses the impact on the economy of current government policies.

In the area of aquatic environment the measure of success/failure becomes the frequency and extent of disasters such as the mercury crisis, the contamination of the Great Lakes with polychlorinated biphenols (PCBs), the fecal contamination of the St. Lawrence River and its tributaries, etc. That these have occurred is a measure of the failure of the system; the frequency and extent of these crises are measures of the adequacy of the system. The ability of government to respond to these crises is a measure of the effectiveness of the system.

Approach Taken

Early in the preparation of the background study it was obvious that water-based research in Canada was highly regional in character and could best be accessed locally. It was also the intent of the study that perceived research needs have a clear basis in real problems. The approach thus took the form of traversing the country, conducting interviews and workshops to identify regional water-based problems. The interviews were conducted January to September 1975, and more than 400 people contributed information and understanding. Field time was divided up regionally: 3 weeks in the Maritime Provinces; 3 weeks in Ontario; 2 weeks each in British Columbia, Alberta, and Quebec; 10 days in Manitoba; 1 week each in Newfoundland and Saskatchewan. An additional 4 months was spent in the Capital Region, part on interviews, part on the correspondence associated with the cross-country visits, and part on preparation of the report. The notes prepared during the interviews held across the country comprised two large volumes. This material, the specific knowledge and reflections of more than 400 people, found expression as the detail that filled out the framework of the report. To identify the sources of information and ideas used in the study, would make the report extremely difficult to read. Need-

less to say, the author is deeply indebted to all contributors. No one who was asked to contribute refused to do so.

Emphasis and Bias

Sources of pollutants can be grouped in two large categories. Point sources are those foci of contamination that can be precisely sited geographically. Typically, this is the effluent outfall of a factory or municipality. Nonpoint sources are diffuse and, hence, not easily identified as to origin. Examples are pesticides, agricultural fertilizer washed into waters, road salt, PCBs, etc.

In early years, virtually all agencies charged with the responsibility of protecting the quality of the aquatic environment, directed their efforts at point sources of contamination. The reasons were many and obvious. First, it was easy to do; that is, it was easier to monitor the flow of waste at the factory fence than to monitor the quality of precipitation in a remote area. Another reason was the ease of dealing with the clientele. For example, it is far easier to force an industrial plant to comply with regulations than industries as diffuse as agriculture, transportation, or forestry. Thus, regulation of point sources offered the greatest pollution control-per-unit of effort expended. This devotion to one category of pollution was not unique to Canada. The U.S. Environmental Protection Agency concentrated all its resources on point-source pollution and was eventually taken to court by environmentalist groups for neglecting others.

In the regional-workshops approach to this study, administrators and researchers, in keeping with the terms of reference, talked mainly about problems not yet tackled or solved. A disproportionately large number of these problems fell in the category of nonpoint sources of contamination. The weight of this opinion then gave the study an obvious bias of concern for additional research on nonpoint sources of degradation of the aquatic environment.

Another corollary of this approach is that the workers interviewed talked mostly about problems that remain to be solved. The overall report identifies areas of weakness and largely ignores areas of strength. It would be unfortunate if the reader gained the impression that nothing is going well in the area of aquatic environmental quality. But the purpose of this study was not to eulogize that which is in order, but rather to make apparent that which is not.

An Ill-Structured Problem

The problems of maintenance of aquatic environmental quality and associated responses fall in Chevalier's category "ill-structured." Ill-structured in that the problems are complex to enigmatic, involve a variety of unrelated approaches, and a plethora of government agencies ranging from unrelated to closely related.

An example of a complex to enigmatic problem is that of mercury in the aquatic environment. Mercury occurs naturally in Canada, and varies considerably in amount locally. Thus, an extensive effort at monitoring and mapping is required concurrent with any assessment of mercury of human origin. The amount of mercury lost to the environment to the present time is not known and corporations are under no obligation to make this information available. Thus, it is not possible to construct a mercury budget for a body of water, calculate clearing times, or such. Furthermore, information on the mercury content of fish analyzed in routine (federal) fish inspection is classified as secret. The combination of these constraints makes the problem so ill-structured it obviates rationalization. The result is no thorough review or overview of the mercury problem in Canada. No analysis of the research effort devoted to mercury can by-pass the enormous constraints described above.

The problem of protection of the aquatic environment is ill-structured in that it involves multiple levels of government and a myriad of overlapping agencies within these levels. Federal and provincial governments both interpret their mandates as including the "environment" and to a different degree in each province. Thus, a problem that is a federal responsibility in one province will be a provincial responsibility in a second, and a shared effort in a third. Environmental concerns researched (by the feds or the provincials) in one province may be regarded as nonproblems in another. Within the federal government, environmental problems transcend the structural units (there is no reason to think that it could be otherwise) and often involve a host of agencies. The effectiveness of a multiagency task force depends, in the first instance, on the willingness of the agencies to interact cooperatively. The application of human and monetary resources is secondary. Examples of struggles between agencies for "responsibility" for problem areas are legion. A classical example is that of Department of Environment and Department of Indian and Northern Affairs vying for responsibility for environmental problems in the north.

These properties — political, ethical, legislative, and territorial — define the form of the problem of aquatic environmental quality. These are what

make it ill-structured and, hence, impossible to analyze simplistically.

The Canadian Paradigm

The way Canadians think about water has been influenced greatly by the amount of water they see represented on maps of Canada and the numerous bodies of standing water they encounter. Further, Canadians have been bombarded with statistics on the proportion of the world's water in Canada, and self-congratulations for being so blessed. Professor F. E. J. Fry summarized this illusion as "the great Canadian fallacy — half the world's fresh water."

In fact, the proportion of freshwater storage in Canada is closer to a third, but this too masks a more important truth. Canada receives a modest amount of precipitation, about 20 inches annually on average (Cass-Beggs 1961). For the entire 3,850,000 square miles of Canada, this amounts to 5% of the total precipitation of 80 billion acre-feet falling on land on this planet (Carr 1966). Canada then receives a modest share of the world's precipitation. What is distinctive about Canada is that it is a cold country and has, therefore, a low rate of evaporation. Canada is very young in the postglacial sense and, thus, has a large number of depressions filled with water. The rate of flow through some basins may be very slow; Lake Superior for example has a flushing rate of more than 900 years. Long filling times for lakes have implications in terms of how much water may be withdrawn and the persistence of contamination. Thus, these freshwater environments of Canada carry with them some special responsibilities. They must be consumed cautiously, and once the quality is impaired, recovery time may be very long.

The Canadian water paradigm varies enormously regionally and the regional differences can be expected to accentuate with shifts in population. Of special concern are the "headwater" provinces of British Columbia, Alberta, and Ontario. These are currently, and are predicted to continue to be, the fastest growing areas of the country (Fig. 1), but are not necessarily the areas of greatest water supply. Ontario, for example, with 36% of the population of Canada, receives only 12% of precipitation. Most of the Ontario population lives in a small area less than 5% of all the settled area of Canada (Cass-Beggs 1961). People in southern Ontario have at their disposal a relatively small amount of renewable fresh water.

Another anomaly is the fate of prairie precipitation. The Prairie Provinces make up almost

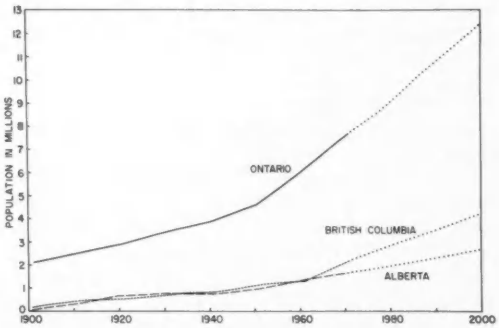

FIG. 1. Real and predicted population growth for British Columbia, Alberta, and Ontario (Statistics Canada).

a third of the settled area of Canada but receive on average about half as much precipitation as the rest of settled Canada. The result of this low precipitation and considerable evaporation is reduced runoff; the prairies average only 2.8 inches or 6½% of the national total. This paucity of water on the prairies has led to agreement among the provinces as to its disposition: Alberta passes on to Saskatchewan one-half of all water that originates in Alberta, Saskatchewan passes to Manitoba one-half the water received from Alberta plus one-half the water originating in Saskatchewan. Two of the fastest growing cities, Calgary and Edmonton, in the country (or world) (Fig. 2), are astride the two most impor-

FIG. 2. Population growth for Calgary and Edmonton, Alberta (Statistics Canada).

tant headwaters on the prairies. These rivers, the North Saskatchewan and the Bow, are not large in relation to the associated populations and industries. The quality of headwaters such as these warrants special concern.

Current Monitoring Programs

Many programs are interrelated. For example, water quality has limited value without some knowledge of quantity. Thus, knowing the chemical composition of a stream at some point in time is of limited value if it is not known if this was low water or high, during a rainstorm or freshet, etc. Similarly, knowing chemical composition but not flow, or flow but not composition precludes a calculation of transport by the stream. The interdependence of monitoring systems is too often overlooked, most commonly because each is housed in a different government agency.

Water Quantity

The agency responsible is the Applied Hydrology Division, Water Resources Branch, Inland Waters Directorate (IWD), Environment Canada. This agency monitors flow in 9 of 10 provinces; Quebec assumed its own responsibility in 1964. Ontario maintains some stations in addition to the federal ones. The backbone of this operation is the coding system defined in 1922 for the identification of gauging stations. The associated maps superficially resemble watershed maps and considerable grief has ensued from the invalid use of the maps for drainage basins.

Discharge data is relatively simple and lends itself to computer storage. Some 133 million characters are now stored. Publication is via photo-offset printing from computer printout from tapes. In addition to the annual printing of data from all stations, a Summary Series is produced every 3 years, covering the previous 20-year period.

It would be desirable if other monitoring programs were tied to water quantity as far as possible, to maximize the use of the interrelated information.

Chemical Quality of Water

It is tempting to state that there is a myriad of agencies collecting data on water chemistry; perhaps it just seems that way.

Under the Canada Water Act, Inland Waters Directorate has the responsibility to determine the base-line levels of water quality throughout the country. This is managed through regional laboratories reporting to head office via an information system, NAQUADAT (Canada Water Resource Branch). The information gathered is published periodically; for example, the British Columbia data for 10 years was published in 1975, the Yukon and Alberta data are in press. In addition, IWD enters into basin studies, usually as cost-shared agreements with the provinces and other federal agencies. These have yielded several detailed reports on watersheds such as the Saint John, Churchill, Nelson rivers, etc.

The role of IWD is to provide background data on the quality of water. Almost de facto this becomes the basis for setting water quality objectives for the watershed. Having done so, the role of monitoring and protection then passes to the Environmental Protection Service (EPS).

Chemical and Biological Assessment of Pollution

The Environmental Protection Service began as the enforcement arm of the Department of Fisheries, that is, to apply the Fisheries Act. One provision of the Act states in effect that thou shalt not put anything in the water harmful to fish. As such, this Act is actually or potentially a powerful piece of legislation. It is not, however, so all-encompassing that no other legislation is needed. The Fisheries Act is not operational (for example) if no fish are present or if the offending material, such as mercury or PCBs, is not toxic to fish, but is toxic to warm-blooded animals that consume fish.

The Environmental Protection Service monitors water quality in the context of specific pollution or contamination. Under the BNA Act this can be, and is, interpreted as either a federal or provincial responsibility. The federal concern has several components. For example, the federal government does not want any part of the country to become a "pollution haven." That is, to encourage dirty industry to operate/locate in a province with lower pollution standards. The federal attitude then becomes one of monitoring pollution at the "factory fence." More precisely, monitoring the effluent from each individual plant. The federal philosophy is that of containment within the plant.

Provincial Pollution Monitoring

The provinces have equivalent organizations, usually within a provincial Department of Environment. The age, strength, experience, and mandate varies greatly between provinces. Many provincial agencies are highly competent. For example, Pollution Control Branch, B.C., has 80-plus people in the laboratory and 60 more in

the field. More than half a million water analyses are performed annually. Every stack and discharge pipe in the province operates under a permit. Each week the Director receives a computer printout of all permit violations in the province, and action can be planned accordingly. Permits are reviewed periodically from the perspective of continued acceptability of the prescribed levels of discharge. The exception is the discharge of industrial wastes into municipal sewage systems. Such discharges are not monitored as they enter the sewer, but monitoring is done on water leaving the waste-treatment plant.

Federal and Provincial Ideologies

This example underlines the profound difference in federal and provincial attitudes: containment vs. dilution. Inherent in the concept of dilution are receiving water standards. It becomes necessary to invent concepts like "assimilative capacities," that is how much of, and what kind of pollutant a receiving water could tolerate. The simplistic assumption being either that (1) to some magical level of concentration there was no effect on water chemistry or organisms and pollution could go on up to that level without difficulty, or (2) the effect of the pollutant was a graded effect and some acceptable level of pollution effect could be defined. For example, a loss of a third of species diversity from a community of organisms might be considered acceptable.

Another mystical concept is that of the "mixing zone." This is the region of receiving waters where pollutants would enter, no pollution measurements would be made, and no enforcement applied. It naturally follows that if unacceptable levels of pollution were detected outside the mixing zone, then the mixing zone was too small!

These concepts of "assimilative capacity" and "mixing zone" were invented and used by lawyers and engineers as if they had some basis in scientific theory. There is nothing in ecological dogma, for example, that says a stream can lose some fraction of its species and maintain its integrity.

Another problem area emerges from the dichotomy of federal–provincial approaches. The federal position requires the same receiving water standards across the country. The provinces want flexible standards because of regional differences in water chemistry (such as hardness, alkalinity), not only between provinces but within them.

The provincial philosophy when applied to industrial and municipal wastes may produce some serious effects. For example, permitting unmonitored industrial wastes to enter sewage may result in final (mixed) wastewater with synergistic toxicants. The heavy metals content of the municipal wastes may preclude the use of this material for fertilizer.

Predictably, it is in this area of environmental protection where federal and provincial governments so often clash. It is here that the Canadian disease the "federal–provincial syndrome" appears most often. The disease is fed in part by the existence of two parallel organizations, a federal and a provincial, with similar mandates and expertise. In some instances the duplication of effort is extensive. The most recent policy of Environment Canada has been to allow the provinces to take on this role when the provinces want it and have the resources to fulfill the mandate.

At this late date, the opportunities for federal research initiatives are limited. Each province has its own laboratory. Almost all have developed their own methods of analysis. Almost all have their own data bases, incompatible with the federal one. Permit systems differ between provinces. Some provinces have their own regulations/guidelines for specific industries. In short, in the absence of early federal initiatives, the provinces went their own way. Provincial monitoring organizations will not easily change their methodology or data bases in response to a federal initiative now.

Several federal initiatives helpful to the provinces have been launched. Canada Centre for Inland Waters (CCIW) provides test samples for all laboratories that wish to participate and publishes comparisons from all participants. The Freshwater Institute and CCIW mount symposia on a wide range of environmental quality topics. The federal data retrieval systems, abstract search service, and pollution abstract service are all available to the provinces. The federal government took the initiative in launching a series of workshops with heavy provincial representation to prepare guidelines/regulations for each industrial group in Canada. The provincial complaint in this case is not that the feds do too little, but rather too much! The provinces are hard pressed to find (and spare) an authority for each of a dozen study teams.

Further federal initiatives are warranted in several areas: (1) To identify ways to reduce the number of samples being analyzed. It is not uncommon, for example, to find that a field technician, who is permitted to spend up to $5.00 a day on his own authority, can collect and submit to his laboratory in a day water samples that will cost $1500.00 to analyze. Water chemistry data collection borders on an obsession in some instances. (2) To provide leadership and expertise

in data interpretation. Only a small fraction of the data now gathered on water quality is analyzed adequately, in the sense of extracting meaning from the data. Putting the federal house in order comes first, then proselytizing the provinces. The route is through workshop sessions, including worldwide authorities as speakers. Hopefully university teachers would be involved to improve teaching of data interpretation in that sector. Finally, the message must find its way to the people in federal and provincial agencies. (3) To minimize the cost of the massive amount of water chemistry necessary, by improved laboratory design, and by reducing the number of laboratories. It was a breath of fresh air to visit federal or provincial laboratories shared by two or more agencies. The territorial imperative was reduced greatly, and cooperation increased accordingly. The efficiency of the many water chemistry laboratories across the country warrants a study in itself. (4) To reduce the country-wide efforts expended on new methods. In almost every lab visited, the statement was made that the existing methods were no good and a large amount of effort had to be devoted to developing new methods. One cannot help but wonder if this is displacement behavior: an opportunity for research and publication in what is an otherwise dull routine. If this is the case, perhaps this effort could be redirected into data interpretation. (5) To better relate the water chemistry data to other environmental concerns, for example, to aquatic organisms and their water quality requirements. This will be difficult, in that the people involved in the fields of chemistry and biology differ in educational experience and are in different departments. Their disciplines must be forced together, as water and oil can be forced together under pressure, but without making mayonnaise.

Early Warning Systems

A specific charge by the subcommittee was to examine the adequacy of early warning systems that might prevent crises such as mercury. There are two approaches to this environmental concern. One is to monitor the environment and look for effects. The other is to license the use of specific materials. Both approaches are in use currently by Environment Canada. In the former approach, measurements have to be made on the "right" substance at the appropriate time and place, and someone must put an interpretation on the data gathered. In the second approach, the toxicity of the substance must be known before it can be written into a license and this requires a sizeable research base. The limitation of both approaches is obviously the enormous effort required to research or monitor the million-plus chemical substances in use by man.

In the case of mercury, the pollutant was without obvious ill effect on the fish accumulating it. Thus, these animals, in terms of survival, growth, reproduction, or behavior, betrayed nothing untoward in the environment. They were useless as indicators. Other environmental contaminants can be expected to behave the same way. For such materials, detection must take other forms, for example, identify all hazardous materials used in our society, their toxicity, use, and disposal. With more than 5000 hazardous chemicals shipped in commercial quantities, this is a monumental job. The alternative is to monitor some substances in the environment or in the organisms in the environment that may be accumulating them. Where human health is concerned, monitoring is the responsibility of the Department of National Health and Welfare. For other organisms it falls to a variety of agencies including Department of Agriculture, Canadian Wildlife Service, and Fish Inspection Branch of Environment Canada.

Water Quality Indices

In reviewing this topic it was apparent that at least four federal agencies were at work on indices of this kind.

Statistics Canada is in the process of generating one or more indices of environmental quality, to be used like the cost-of-living index as a measure of the relative well-being of the environment with reference to specific localities, notably large urban centers.

The Planning and Finance Service of Environment Canada has produced a composite environmental quality index (Inhaber 1974), although this has not been used subsequently.

The Economic Council of Canada devotes a considerable portion of its annual report to social indicators. One, treated for the first time in the 11th Annual Review, was urban air quality. This is preceded by an interesting rationale for currently concentrating on air rather than water quality: water pollution can often be avoided (e.g. don't swim) but breathing is unavoidable. For millions of people in Quebec whose streams, rivers, and lakes are too polluted for water-based recreation, this is sage advice but small comfort.

The Inland Waters Directorate of Environment Canada has a mandate to produce water quality indices. The first step is a statistical approach with a more limited objective of indicating

whether the quality of about 10 major water courses is improving or deteriorating.

By no means are these all the individuals or agencies involved in producing indices of this kind within the federal government or outside it. It may be appropriate to: (1) assemble all interested workers in a workshop atmosphere so they will know what each is doing, and (2) review within the government the responsibility of coordinating these scattered overlapping efforts.

Indices are of two types, descriptive and predictive, on the basis of use, rather than inherent properties. Indices also may be simple, that is based on a single variable, or complex when a number of variables are pooled, with or without individual weighting. The measure of coliform bacteria as an index of fecal contamination is an example of a simple index. Slightly more complex is Ryder's morphoedaphic index combining the positive effect of dissolved solids and the negative effect of the mean depth of a lake, to yield an index of fish production (Ryder et al. 1974).

The more simple the index, the more operational it becomes; the more complex, the more it becomes an abstraction that cannot be related to the real world. This is due in part to the difficulty of combining incompatible components into a complex index. *Escherichia coli* is a basis for indexing the suitability of water for human use, with low–good and high–bad for man but of little importance to fish. Increasing dissolved solids (up to a point) tend to be good for fish and bad for man. Waters intermediate in both variables may be acceptable to man and fish. But the linearly combined index may be a value indicating the water is simply unacceptable in total. This is the parallel situation to the cost-of-living index. It is of no value to the consumer to know that the index has remained constant without knowing that this is achieved by substituting poultry for beef in the market basket when the price of beef rose.

The purpose in developing this argument at such length is to make evident the great difficulty in producing a water quality index of widespread value. A simple index or one involving a few variables may have considerable predictive value within a single body of water or watershed. It is very difficult to visualize an index or indices applicable to Canadian waters in general and retaining any predictive value. In short, who is going to use such an index and for what?

Water Quality Atlas

As with any map, the first question is, who are the potential users of an atlas of water quality? The second question is, how much information does the user need? The third question is, what is the cost of providing this service in relation to the value to the user? Finally, what is the life expectancy of the information contained in the map?

The extreme choices are to represent all the country on a single small sheet of paper or to produce a great many maps in detail of the topographic series (17,000 to cover Canada at 1:50,000, 918 maps at 1:250,000). An example of the former is the Water Atlas of the United States which indicates pollution in major watersheds, chemical composition by physiographic regions, etc. An atlas of this type has value in education and in broad areas of policy making. It has, however, limited use in dealing with problems within watersheds, that is, the detail simply isn't possible. Such simplistic or superficial presentation may be misleading. The Maitland River (southwestern Ontario) is reasonably good in terms of quality, but in summer the flow may fall to zero.

Preparation of maps is time-consuming. Five to 7 years is required to produce and inspect a topographic map prepared from aerial photographs. Geographic features tend to be long-lived, and a 10- or 20-year-old topograph may continue to be a useful document. Water quality, however, is changing rapidly in terms of increasing industrialization, stiffer standards and regulations, improved technology for maintaining water quality, etc. Clearly a water quality atlas prepared two or even one decade ago would have limited value today.

These problems of scale and chronology could be solved by producing two different publications. The first would take the form of a series of water quality maps included in the Atlas of Canada. This publication already has 24 pages concerning water, and thematically water quality would fit well in this section. The Atlas has a number of advantages: an experienced production staff is operating continuously; a revised version, requiring 30 man-years, is produced every 5 years (next edition due in 1979); individual maps are sold as separates at low cost through Supply and Services Canada, Printing and Publishing. Finally, the Atlas is widely distributed in libraries, especially school, public, and government, which could be expected to be the greatest users.

Beyond the single sheet maps of all Canada, water quality will probably be mapped on several scales depending on the nature of the problem. For example, agencies within the provincial governments frequently record water quality or like data on the Applied Hydrology Division maps

used for defining monitoring stations. The attendant system of defining monitoring sites in Canada has been adopted by the Water Quality Branch (IWD, Environment Canada) and several provincial agencies. This scale of mapping is better suited to the needs of the regional planner. Beyond this, topographic maps exist for the country in scales of 1:50,000 and 1:250,000. In both cases, the final map is the product of six or more printings. It is not profoundly difficult to modify/prepare one more plate in such a series that would add to the map data on water quality. Such maps would only be prepared when the problem warranted treatment on this scale. One could visualize the value of such maps in areas of most serious human impact: the Fraser Valley, Edmonton–Calgary belt, southern Ontario, St. Lawrence Valley, Saint John Valley, etc.

Finally, computer-directed automated printing can be used to produce acceptable maps in short periods of time. The information content may be limited by the capacity of the equipment. Also a large amount of work is involved in preparing the data for computer use. This technology is underutilized for water quality mapping at the present time.

Constraints

Corporate Morality

One constraint to the solution of environmental problems is the desire of industries to keep secret information vital to any understanding. An example is the Domtar plant in northwestern Quebec. The amount of mercury lost from the plant has been estimated at 16,000 pounds (Canadian Press, Oct. 16, 1975). Domtar alone knows how much mercury was purchased to replace losses, has not made this information public, is under no legal obligation to do so, and accepts no moral obligation to do so. The suggestion has been made that the 8 tons of mercury might have "evaporated" (Ottawa Citizen, Oct. 16, 1975). It is difficult to imagine how this could have happened without endangering the health of the plant workers or why the company would permit mercury worth a third of a million dollars to evaporate. It has also been suggested that the mercury in fishes of the area, being organic mercury, could not have come from the inorganic mercury that escaped from the plant. That microorganisms convert inorganic to organic mercury has been known since 1969. Knowledge of the amount of mercury lost into the environment is essential to understand the problem, most particularly the preparation of a mercury budget for the basin and preparation of a predictive model of recovery.

Another example is the stack at Copper Cliff, where large amounts of metal are carried aloft and fall on the surrounding land and water. The company (INCO), the federal and the provincial governments, have all determined the composition of the stack effluents. Extreme secrecy surrounds all analyses. The best data available is for 1971: 14,500 tons iron, 2000 tons nickel, 1800 tons copper, 155 tons zinc, 12 tons cadmium, 240 tons lead, 110 tons arsenic, and 17 tons selenium (Steel Labour Oct., 1973). Again ecologists need to know what and how much is emitted to model the response of the ecosystem to the loading of toxic materials. The purpose of understanding the degradation of the environment is to foretell what this implies for the health and survival of man and other organisms. In the current array of value judgments this is considered less important than secrecy.

Secrecy

Within Environment Canada excessive and unnecessary secrecy surrounds much of the data on the environment. This is viewed as a major constraint in the search for understanding of the effects of contaminants on the aquatic environment. Within the terms of reference of the present study, establishing the adequacy of both analysis and interpretation becomes very difficult. Fish Inspection Branch, for example, maintains sizeable laboratories across the country to analyze freshwater and marine fish and shellfish landed by Canadian fishermen, and similar products imported into Canada. The results of many of these analyses are secret and are not available even to other researchers within the same service. There is no way of knowing, except for Fish Inspection Branch, whether the analyses or interpretations are adequate to achieve the objective. The best way to ensure this adequacy would be to make public the reports based on the analyses. This would at least provide a strong incentive to maintain high quality work.

Parenthetically, the present system of keeping the results of fish inspection data secret is extremely wasteful of federal resources. Many other agencies require the same information in the legitimate development of their own mandates. The result may be two laboratories side-by-side generating the same data, at least in part. Oftimes other agencies are obliged to turn to less satisfactory measurements of environmental pollutants. Thus, when the International Joint Commission was refused data on contaminants in Great Lakes fishes, it was obliged to launch a costly and not altogether satisfactory alternative

study of contaminants in fish-eating birds and mammals.

Finally, and most relevantly, authoritarianism of any kind results in less successful problem solving. Popper (1966) argued that a society could most effectively solve its problems openly. Specifically, by unrestricted generation of a variety of solutions, their public criticism, followed by selection and modification on the basis of that criticism. This being the case, and the argument of Popper has never been refuted, authoritarian/secretive analysis or interpretation of environmental data can only be less effective than when done openly.

The author of the present report cannot advise the subcommittee as to the total adequacy of the early warning system.

In light of the above, the present policy of secrecy should be reexamined.

University Role

The university sector is making a relatively small research contribution in the area of aquatic environmental quality. There are few centers of concentration and those are more apparent than real. A few exceptions are to be found.

One field station was staffed by 2 professors, 10 graduate students from the University of Manitoba, 6 professors and graduate students from Columbia's Lamont Observatory, and 6 technicians. The equipment was good to excellent, and operating support adequate. The seminar series was the most intensive in the country. Direction of graduate work was exceptional and the choice of research projects outstanding, in that all studies were at the forefront of human knowledge. One hesitates to identify the Experimental Lakes Area (ELA) Station lest it be ruled contrary to the BNA Act and we lose our most outstanding research station for graduate work in limnology. But the lesson is clear: universities are too poorly financed and have few people of the skill and drive of Dr D. W. Schindler to mount a first-rank research effort on water.

Another academic area of concentration is INRS-Eau at the Université du Québec. About 80 people are working in facilities at Complex scientifique. One quarter of the organization's operating budget is derived from the University and the remainder through contracts from various governments and industry. The organization offers a graduate 2-year multidisciplinary program in water, the only one of its kind in the country.

This report does not presume to define the role of the university sector. It does, however, acknowledge that there is a divergence of opinion as to how much, and in what form, the universities can contribute to the study of environmental quality. The university role is perceived as being restricted to teaching (Meyboom 1972), to offering an unique vehicle for solving interdisciplinary problems (H. F. Fletcher, personal communication). In general, academics express great difficulty in separating two activities, graduate teaching and research, but financing for these activities are primarily provincial and federal, respectively. Further, the interface between universities and government is poorly institutionalized. During this study the commonest complaint by academics was that they never knew who they were to contact/deal with in government in relation to environmental research.

The great bulk of university-based research on water could be best described as artisanal science. It is characterized by isolated and unrelated works, for example, one worker studies the benthos of one stream, another the organics of a second stream, a third the inorganics of a different stream, another worker the fishes of a nearby river. Each worker has a rationale for doing his own thing where he chooses, but collectively the bits and pieces add up to far less understanding than if all effort had been directed at a single study area, such as a basin or watershed. This is not to imply that all university research must be part of some master plan. Indeed, the university is the logical place for doing much innovative work.

Perhaps university researchers would be better financed if more of their work was innovative rather than monitoring. A large proportion of university-based research takes the form of primary data collection. In some cases, large sums of money are expected on monitoring environments that are costly to work in or where measurements are costly. Thus, the Great Lakes Institute struggled for years to maintain a monitoring vessel on the lower Great Lakes. (A Lesser Lakes Institute would have been more appropriate to the teaching mandate of the University of Toronto). Similarly, the Kananaskis Centre is involved in conducting large numbers of regular chemical analyses, organic and inorganic, on water quality.

The corollary of this obsession with the technology and mechanics of primary data collection in university programs, is the scant attention paid to data analysis and interpretation in the educational process. This explains, in part, the weakness of data interpretation in many aspects of water-based research within federal and provincial governments. That is, university graduates employed by governments are obliged to work

much of the time with existing information. There could be more in their university training to help them in this role.

This weakness of information analysis and interpretation has another kind of root. Very few Canadians have pioneered in this field. Rare is the university professor who has developed a new approach and a group of disciples to carry the message. This is in contrast with other countries, including some small ones, where such people have emerged. The approach developed by Lance and Williams (Australia) for the analysis of complex biological communities is a good example. The literature abounds with the names of people and places: Jaccards Index, Canberra Metric, Shannon-Wiener Function, Manhattan Metric, etc., outside Canada.

It is desirable that the six 5-year grants to universities be reviewed to assess the successfullness of the experiment. It is essential that the reasons for failure be identified where the large input of federal funds has not resulted in a continuing program. Conversely, in those centers that are alive, the strengths should be documented. This information collated into a report would serve as a guide both to universities and government where similar team approaches are advocated in the future.

University Research Funding

The inability of universities to mount effective programs on aquatic environmental quality is hardly surprising. Financing for university research is provided primarily by the National Research Council of Canada (NRC), and funds for grants-in-aid of research have been frozen since the latter half of the 1960s. In the years since then, attrition through inflation has been severe, with the loss of more than a third the value of research funding in the period 1969–74 (Fig. 3). This policy has not been pursued in other industrial nations (Fig. 4).

University research in the natural sciences for most of a decade has been starved for funds in Canada. Even more obviously, university funding has been starved relative to federal in-house research spending in science (Fig. 5).

Within the NRC grants-in-aid program, relatively little of the $71 million (1973–74) was expended on research into aquatic environmental quality. A review of titles listed in the 1973–74 Annual Report on Scholarships and Grants in Aid of Research yielded 18 projects totaling $118,155 (Appendix 1) or ⅛ of 1% that could be considered to be in this category. Another 17 grants were for studies which in part may have involved aquatic environmental quality. Whatever the reasons, NRC grants-in-aid are not a major source of funding for research of this kind in Canada. However, a few sizeable development grants were made (Appendix 2).

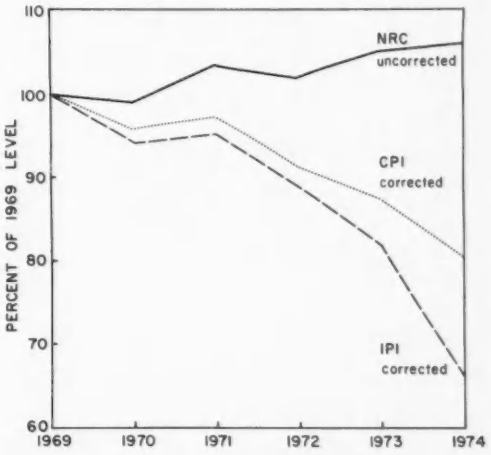

FIG. 3. National Research Council of Canada, science research funding to universities expressed as a percent of 1969 level, and corrected for inflation using Consumer Price Index and Implicit Price Index (CPI and IPI courtesy Statistics Canada).

Funding was made available for research on water in 1968–69 by the Department of Energy, Mines and Resources (EMR). This responsibility was moved to Inland Waters Directorate, Environment Canada, and funding continued for the 5 years of agreements. The federal funds, a maximum of about $865,000 annually, led to the formation or continued support of centers at six institutions: Westwater at the University of British Columbia, Hydrology Division at the University of Saskatchewan, the Agassiz Centre at the University of Manitoba, Waste Treatment Processing at McMaster University, the Institute for Environmental Studies at the University of Toronto, and the CENTREAU at Laval University. Since the end of the 5-year grants, most centers have very limited support and perhaps half of the six will cease to function.

Basic to the kinds of problems described above, and largely responsible for it is the relationship between the federal government and the universities. The British North America Act defines education, including university education, as the responsibility of the provinces. The provinces have agreed, albeit reluctantly, that research within tertiary education could be funded federally. There is, however, no single federal agency

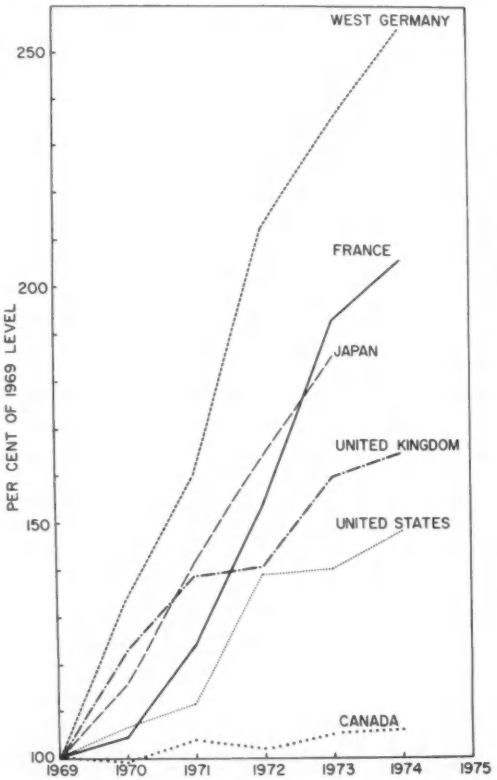

FIG. 4. Support for science research in universities, six industrial nations, 1969–74, calculated as percent increase since 1969.

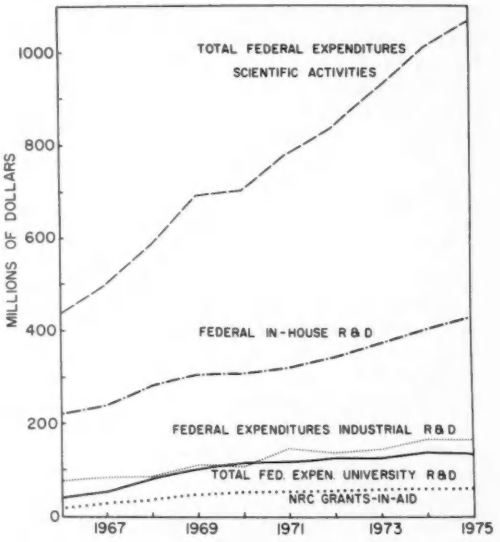

FIG. 5. Comparison of federal expenditure on R&D by sector of performance (Statistics Canada, Cat. No. 13-202).

charged with this responsibility, with the result that each government department or unit within a department establishes its own granting operation. The objectives, approaches, and amounts of money so committed vary greatly between granting agencies. This is apparent in Table 1 in the amounts and percentages of expenditures through the university sector by services in Environment Canada.

Of the total expended for research and development through the universities, 67.3% is by Environmental Management Service and most of this by Inland Waters Directorate. The Fisheries and Marine Service, with a much broader mandate (eutrophication, marine and freshwater biology, marine and freshwater fisheries) accounts for only 16% of the research sponsored by Environment Canada in the universities.

Municipal Waste

In many areas of Canada, domestic sewage is the greatest single cause of reduction in the quality of the aquatic environment. The loss of quality affects man and organisms directly, and the use of plants and animals for human food indirectly.

The problem of disposal of human wastes is an old one. It took on a new urgency with the invention of the flush toilet by William Crapper, as this committed human waste to disposal in water. Modern sewage treatment was devised by Edmund Chadwick in 1843, employing the concepts of lagoon settling and oxidation of high oxygen-demand material. Since that time research into waste disposal has been remarkably modest.

Even more remarkable is the fact that 130 years after Chadwick demonstrated the value of waste treatment, many population centers in Canada, a country with one of the highest per capita incomes in the world, still discharge untreated wastes into ground and surface fresh waters and estuarial and marine waters. This action carries with it risks to health, reduction in environmental quality, and sizeable economic losses that are often ignored.

Treatment and Nontreatment

In general, disposal of domestic and industrial sewage waste is more common and more sophisticated in the interior of the country than in coastal or near-coastal areas. In Alberta all sewered communities have treatment to the equivalent of the secondary level. In Saskatchewan all communities

TABLE 1. Department of Environment expenditures on scientific activities, 1974–75. (Source: Statistics Canada)

Service	Total expenditures	University sector	Percent university
Atmospheric environment	69,842,000	615,000	0.88
Environmental management	79,805,000	2,623,000	3.28
Environmental protection	4,190,000	37,000	0.88
Fisheries	25,248,000	420,000	1.66
Marine	52,268,000	205,000	0.39
Total	231,353,000	3,900,000	1.68

have primary treatment and more than 90% have lagoon treatment with semiannual discharge, that is, the equivalent of secondary treatment. Chlorination is used in communities like Regina and Saskatoon with other communities downstream, and especially North Battleford where the sewage outfall is upstream from the domestic water intake. In Manitoba, 85% of communities over 200 people are sewered and effluent-treated. A few municipalities have inadequate systems, but most deficiencies are being up-graded.

This high level of treatment in the Prairie Provinces is in sharp contrast with the province of Quebec. A mere 11% of domestic wastewater receives as much as primary treatment (Association québecoise des Techniques de l'Eau 1975). Virtually all streams and rivers entering the St. Lawrence River between Valleyfield and Quebec City are contaminated by sewage. All beaches along the St. Lawrence in the vicinity of Montreal are closed to swimming. Until recent decades the waters and shores of the St. Lawrence were a great recreational resource, readily accessible to a large number of people at low cost. Now the St. Lawrence ranks with the Mississippi and Rhine among the most polluted rivers in the world (Ottawa Journal, Aug. 22, 1975). Similarly, many rivers and streams of the St. Lawrence Valley provided convenient water-based recreation. Now rivers like the Yamaska have 3–4 ppm available phosphate from farm and domestic effluent, with the predictable growth of algae.

Given such universal pollution of fresh water, the attitude that pervades the residents of the St. Lawrence valley is that their community can do nothing alone, and that local improvement is pointless if pollution is not stopped upstream. This rationalization for inaction was broken recently with the federal–provincial–municipal agreement on financing the cost of collection and primary treatment (with chlorination) of Montreal sewage. This is obviously an important first step, but neither primary treatment nor chlorination can be construed as a very satisfactory solution to the problem. Occasional "spills" of chemicals point up some of the weaknesses of domestic water supplies. In August 1975, 68.1 kg of the insect repellent neopentyl glycol was spilled into the Ste-Thérése sewer where it reached a concentration of 8.0 ppm. The water intake, 90 m distant, drew enough of this material to give a concentration of 1.6 ppm in the community's potable water supply.

In general, sewage pollution extends to the lakes of the eastern townships, and the accessible lakes of the north shore as far east as Quebec City. Again there has been a serious loss of water-based recreation, with the high *E. coli* levels precluding the use of lakes for body-contact sport, drinking water supplies, etc. Attempts are being made to improve the quality of some bodies of water. In the case of Lake Memphremagog, a mill on the U.S. side is installing tertiary treatment, and communities on the Canadian side will install sewage treatment.

In the Atlantic coastal provinces several large communities, notably Halifax–Dartmouth, Moncton, and St. John's are without treatment of any kind. In addition, a large number of smaller communities discharge untreated sewage directly into tidewater. At the time this was written, three communities, including Edmundston on the Saint John River, lacked treatment. Some river communities are the nemesis of the sanitary engineer; housing strung out along the shore too far apart for economic sewage collection and too close together for safe use of septic systems.

SEWAGE AND SEAFOOD

The costs of sewage treatment are easy to calculate, but the costs of nontreatment often are much more elusive. For example, how do you assign a dollar value to lost recreation? To aesthetic displeasure? One situation where economic loss due to pollution can be measured is the contamination of food organisms. Common U.S.–Canada standards have been set for acceptable levels of *E. coli* in shellfish, thus simplifying regulations for harvest and export–import. These

standards may be exceeded in shellfish exposed to raw sewage and such areas are closed to commercial harvest. In the Atlantic provinces, the 211 closures extend over an incredible 1800 km^2. That is, these food resources are lost to the commercial fisherman. In practice, some shellfish are moved physically from polluted to nonpolluted areas and held in the cleaner water until the *E. coli* count falls to an acceptable level. (Presumably disease-causing bacterial and viruses are also lost from the shellfish at about the same rate.) At the end of this period, about 6 weeks, the shellfish may be harvested. Filtration rate in oysters varies with temperature, and "clearing" times are much longer at low temperatures. This transfer of polluted shellfish is costly in that it is labor-intensive and not practiced widely. Most closed areas remain a complete economic loss.

Pacific closures are neither so numerous nor so extensive in area. These include Nanaimo, Ladysmith, Crofton, Cowichan Bay, Ganges Harbour, Schwartz Bay, etc. Again the loss of the clam and oyster areas for recreational or commercial harvest is regrettable.

The management of shellfish, meaning oysters, clams, mussels, and quahogs (but omitting lobsters and pectens) is undoubtedly more sound than this section might convey. There has been no serious incident of shellfish poisoning since 1972. At that time some 450 people were known to become sick from eating Caraquet (N.B.) oysters. This coincided with the overflow of a lagoon of wastes from a 1000-pig piggery entering the marine environment. Because of the time-lag between pollution and reports of illness, a cause/effect relation was not demonstrated conclusively.

There are obvious research needs associated with shellfish and sewage pollution. One is to determine the fate not only of *E. coli* but of human pathogens, both viruses and bacteria, in oysters. Are these pathogens stored in oysters? How effectively are they flushed out in clean water? Another very important problem to be solved is the level of sewage treatment necessary to achieve a low *E. coli* level in oysters. Is secondary treatment as is now being widely installed in the Atlantic provinces sufficient to do this job?

The habit of eating raw oysters will not change easily. This carries with it a need for special vigilance in monitoring and an especially secure research base for management.

The relation between sewage polluted water and the edibility of fish is less clear. This is due to several factors: most fish are not filter feeders in the same sense as shellfish. Fish are much more mobile, hence it is difficult to correlate cause and effect. Unlike oysters, fish are almost always cooked with the associated death of contaminating organisms. Finally, perhaps fortuitously, some fish species, like Pacific salmons, that come in lengthy contact with polluted water such as the Fraser River, are the fish almost always canned. This involves pressure-cooking at high temperature and the destruction of contaminating organisms.

Yet another concern with sewage pollution of sea water is the subsequent use of sea water for food processing. Fish processing plants for example are scattered along the coastline of the Atlantic provinces. Such plants tend, of course, to be associated with communities, the community using ocean water for waste disposal and the plant using sea water for wash water. Such use is monitored for *E. coli* and pretreatment of sea water may be necessary.

Chlorination of sewage wastes destroys a high percentage of *E. coli* and hopefully an equally high percentage of bacteria and viruses injurious to human health. It does not, of course, lessen the nutrient content of the effluent in the way treatment does. Cities like Montreal and Vancouver, discharging sewage into fresh water, have opted for chlorination. Traditionally fisheries people have objected to chlorination because of the high toxicity of free chlorine and the resulting compounds like chloramines to fishes (Servizi and Martens 1974). The established method of dechlorinating sewage to render it nontoxic is about four times as costly as the original chlorination and is prohibitively expensive. The International Pacific Salmon Fisheries Commission has been researching the problem of inexpensive dechlorination, and met with some success. It is noteworthy here that the agency trying to maintain environmental quality is obliged to do the research; not just the research essential to the protection of the resource (i.e. toxicity studies) but also the research into a methodology of sewage treatment less damaging to aquatic organisms.

Recently, concern has been expressed that some chlorine and organic compounds resulting from chlorination of water are carcinogenic in man. At the time of writing, it was too early to even hint how this may influence thinking about chlorination of sewage. It can be anticipated that a considerable research effort will be made in this area, much of it outside Canada.

On-Land Disposal

With increasing treatment of municipal waste, the problem of sludge disposal becomes more

acute. As these nutrients originated on land, the ideal would be to return this material to the soil surface. This is often impractical simply because of distribution costs. Beyond this there are very practical problems. We do not know the fate of bacteria and virus particles in sludge, for example, used for growing crops for direct human consumption. Do these organisms find their way into root crops, for example? Ironically this specific area of research in Alberta was aborted when federal funding was withdrawn.

Another problem with the use of sewage sludge is the high level of heavy metals in the material and the subsequent uptake of these metals by plants. The high level of metals comes about primarily through industries releasing plant waste into municipal sewers. The organic matter serves in part as a trap for metals. The provincial–municipal concern is for the level of metals in the effluent leaving the sewage treatment plant, as opposed to the federal stance, which is containment of wastes within the individual industrial plant. Generally speaking, the provincial attitude has prevailed.

Some new approaches have appeared, especially in southern Alberta. Spray irrigation with sewage–lagoon material has been attempted and has proven to be economical. Only forage crops have been grown on this treated soil and there has not been a buildup of heavy metals in animals or dairy products.

This is an area with a range of research needs. Certainly any municipal waste that can be applied to land helps to protect the aquatic environment. Leaching of this material (Great Lakes Water Quality Board 1973) needs to be understood to write regulations governing such "waste" disposal. The sources, uptake, and fate of disease-causing organisms and heavy metals need to be understood. Finally, we know that municipal sewage plants are releasing appreciable amounts of heavy metals into receiving waters. How serious this problem is, has to be determined.

Agriculture

Agriculture has the reputation of being the greatest water hog of all (Carr 1966). Direct demands for water are high for irrigation, stock watering, etc., and may also be high for waste removal such as runoff from feedlots. Some farming practices, especially potato culture, can result in large amounts of soil being washed off fields and entering water courses. Chemical fertilizers similarly may be washed off the soil and enter fresh water. This enrichment increases production of algae, detracting from the quality of the water for many other purposes. Finally, many chemicals used in agriculture, particularly biocidal agents like insecticides, herbicides, and fungicides, enter fresh waters in part, accumulate in organisms, and may become highly concentrated in animals at the top of the food chain.

Soil Erosion

Prior to settlement, the southern portion of eastern Canada was a mixed forest of hardwoods and white pine. The forest floor was covered with leaf litter on a few inches of humus. This black humus owed its existence to an annual deposition of leaves, bacteria-inhibiting acidity, and the presence of organic compounds like tannins. The force of the rain was moderated by forest cover and leaf litter. The organic matter of the forest floor had a large capacity for water retention. Thus, raindrop impact erosion and sheet erosion were limited greatly.

Early settlement took the form of clearing the hardwood forests for agriculture. The thin humus was cut off from further supply and the carbon was quickly consumed by bacteria. The exposed subsoils, such as fine clays, were available for and prone to water transport. The result has been the movement of large amounts of soil into streams, rivers, and lakes. The extent to which this happens is a function of the slope of the land, the porosity of the soil, whether the soil is protected by the crop under cultivation, etc. The increase in erosion with removal of forests and use of the land for row crops has been determined by the U.S. Department of Agriculture at 100- to 10,000-fold. For grassland the increase is 20–100 times (Brown 1968). Figures for total soil transport are not available for Canada. In the United States annual transport by rivers is one billion tons, half of which is carried by the Mississippi River and its tributaries (Gottschalk and Jones 1955).

Potato culture is one of the most damaging types of agriculture in terms of erosion. Soil loss on a 12% slope may reach 10–12 tons/acre per year. The life expectancy of such farmland is between 2 and 3 decades. The cause is primarily that the soil is exposed for all but a small part of the year. Erosion is enhanced further by plowing up and down hills, removal of hedgerows, the use of top killing chemicals, etc. It is not easy to assess the impact of potato farming on the Saint John River or on the streams of Prince Edward Island, but it is clear that the effect is considerable.

Draining Wetlands

Perhaps the second stage in early agriculture

was the identification of periodically or continuously flooded land that could be drained for cultivation or pasture. In southern Ontario, 75% of original wetlands have been drained to the present time. Wetlands have a large storage capacity for water, accepting floodwaters each spring and periodic heavy rains. The effect of such wetlands is to moderate flooding greatly by reducing peak discharge, and extending the duration of stream and river flows. The loss of wetlands has accentuated the process of periodic flooding. And, of course, the occupation of such reclaimed wetlands adds to the damage done by flooding.

In Western Canada, wetlands in the form of sloughs or potholes continue to be drained at a significant rate. This process is largely under the control of the individual farmer. It is to the farmers' immediate advantage to maximize his land under cultivation. The use of ultrawide implements, like 40-ft cultivators, is comprised when sloughs interrupt the linear movement of the equipment. The farmer responds to these incentives by draining sloughs if possible, for example, through temporary ditches made each fall with the plow. Provincial departments of agriculture may also make funds available for more major ditching. The federal Department of Agriculture offers advice and encouragement on slough draining (Korven and Heinrichs 1971). In addition to partial or total drainage of wetlands, it is to the farmers' advantage to remove the copse of woods from around the slough and to burn off vegetation of the basin in the fall. This will permit cultivation closer to the water, especially in the event of a dry spring.

The effect of the above has been the loss of about 1%/year of prairie wetlands during the postwar decades. The loss of cover plus nesting material through burning has an additional adverse effect on waterfowl. Clutch survival of early nesting birds such as mallards is very low under these conditions, but the survival of a second nesting on average is good. Removal of cover from the edges of prairie potholes may increase the effectiveness of predators such as coyotes, foxes, skunks, etc., in their search for the eggs and young of nesting waterfowl.

The total effect of wetland drainage on the prairies has yet to be documented. Removal of cover, especially aspen and willow, reduces the amount of snow trapped in the immediate area of the slough. This in turn alters the pattern of water storage and stream discharge. Yet to be assessed is the change in microclimate with loss of cover and loss of stored water. Finally, the role of prairie potholes in aquafer regeneration is inadequately understood.

Irrigation

The concern for the impact of irrigation on aquatic environmental quality centers on two effects: the amount of water consumed and the quality of water returned.

It almost invariably follows that irrigation will be practiced in areas of low precipitation, high temperatures, and high evaporation, and where surface water supplies are modest. In Canada, such areas are the southern interior of British Columbia and the southern prairies. Alberta and British Columbia account for 73% of total lands under irrigation in Canada (Table 2). Considerable expansion of irrigation is planned for southern Alberta and a lesser amount for southwestern Manitoba.

The immediate impact of irrigation is to reduce the amount of water in streams and rivers. Farmers obtain a license or permit to remove a given amount of water from a stream. All too often these have been issued in excess of the amount of water in the stream. In some provinces for example, permits were issued for a total removal equal to the average annual flow. In summer when demand is greatest, the discharge is typically well below the annual average. The entire stream may thus be used for irrigation. The quality of the aquatic environment ceases to have meaning when the quantity approaches zero. Attempts have been made to safeguard the integrity of a stream by asking for a guaranteed minimum flow, or by requesting a permit for water in the name of the trout living in the stream, or in the name of the fisheries agency. These attempts to establish "rights" for a stream have met with very limited success.

Throughout much of the prairie region of Canada where irrigation is practiced, the salt or soluble solids level of the soil is high. As a consequence, irrigation must be practiced in such

Table 2. Farmland under irrigation in Canada 1970. (Source: Statistics Canada)

Province	Acres
Alberta	537,321
British Columbia	220,987
Ontario	99,472
Quebec	92,895
Saskatchewan	77,489
Manitoba	7,330
New Brunswick	3,129
Nova Scotia	1,866
Prince Edward Island	541
Newfoundland	123
Total	1,041,153

a way to carry off not only the salts in the water, but also those accumulated in or on the soil. The surface runoff from such irrigation typically contains dissolved solids at 2 to 4 times the original concentration. The salinity of surface waters thus is increased greatly. In the southwestern U.S., such high salinity waters cannot be permitted to reenter the Colorado River, as the river water would be unacceptable for use further downstream. Such high-salt waters are collected, like so much sewage, and diverted seaward in canals.

Such an extreme case as described above is not likely to happen on the western plains. But it is important to recognize the extent to which water quality will be affected by irrigation practices. Only limited information is available on this problem in Canada.

Groundwater

Considered overall, the supply of groundwater in Canada is not great. Much of the country is closely underlaid by granitic rocks with little or no water storage. The above notwithstanding, ground water is of great importance in many areas of Canada. In Quebec some 450 small communities and innumerable farms use well water for domestic purposes. Prince Edward Island is totally dependent on groundwater for domestic use, including the city of Charlottetown. In Nova Scotia, only the Halifax–Dartmouth area is supplied with surface water. Half the population of Newfoundland is concentrated in the northern third of the Avalon Peninsula and many of these people, for example around Conception Bay, are dependent on well water. Contamination of groundwater in this area is all too common and a potential health problem exists.

On the great central plains groundwater is the commonest source of supply for rural residences and small communities. The dissolved solids of such waters are high in many areas of the south and south-central prairies. Salts in excess of 1000 ppm render the water unacceptable for domestic use, for watering stock, and for irrigation. Such well water discharged into surface waters reduces the quality of streams. A similar problem with the quality of ground water exists in the area southeast of Montreal. The salt content of the water is high, more than 1000 ppm, due to the presence of some old sea water. Cows watered with such groundwater produce saline milk which dairies will not accept. Hence, the supply of well water is useless.

An obvious research need is to establish an inexpensive method of desalinating groundwaters, in particular in units suitable for operation on an individual farm. The Saskatchewan Research Council has pioneered techniques in this area such as freezing groundwater outdoors in winter. This method may reduce dissolved solids from 4000 to 1000 ppm, but research and development is far from complete.

Livestock and Feedlots

Farms in Canada carry about 15 million cattle, 6½ million pigs, 800,000 sheep and lambs, 37 million chickens, and 342 thousand horses (Statistics Canada). These animals generate 150 million tons of solid waste and 60 million tons of liquid waste annually (calculations based on American Chemical Society 1969). This waste loading is equivalent to a human population of about 70 million people.

By no means all this waste enters fresh water, but a substantial part of it does. Feedlots in particular contribute disproportionately large amounts of waste. The operator prudently locates his feedlot on the banks of a stream to provide his stock with water, and feeding takes place there. During periods of runoff, especially in early spring when the ground is still frozen, liquid and solid wastes enter the streams. This is especially marked in southern Alberta, and this single agricultural practice is the dominant mechanism determining water quality in some watersheds.

Another aspect of the high-density accommodation of cattle along a stream is the impact these animals have on the physical form of the stream itself. Banks are continually broken down and the sediments riled up, rendering the stream a less suitable habitat for aquatic life.

Little work has been done in Canada to assess the impact of agricultural practices, such as location of feed lots, on the aquatic environment. In some provinces guidelines and regulations are emerging, but the research basis for these and monitoring the results of such regulations, remain very modest.

Regulation of the feed lot industry is neither simple nor automatically effective. The number of cattle permitted may be stated on the permit issued, but there is little inspection to verify that this number is not exceeded. Punitive action is rarely taken, simply because the qualifications on a permit such as number of animals, is so arbitrary. That is, how could one convince a judge that 300 head were acceptable, but 305 or 400 or 1000 were not? The data base is inadequate for the protection of the aquatic environment in many respects in relation to the cattle industry.

Fertilizer

It is difficult to define the scope and nature of

chemical fertilizer use in agriculture and the impact on the quality of fresh water. Production (1974) was 12,310,000 tons and domestic sales were 1,827,000 tons. Application varies greatly depending on the value of the crop grown, the nature of the soil, etc. The Holland Marsh at the south end of Lake Simcoe, Ont., is an extreme example. The soil is the organic matter of the drained marsh, rich in carbon but deficient in most other plant nutrients. Chemical fertilizer is applied to the 6000 acres at an average rate of 500 lb/acre, and as high as 800 lb/acre. A fraction of the 3 million lb so applied is washed from the soil, enters the drainage canals, and ultimately the south end of Lake Simcoe. Nicholls and MacCrimmon (1974) measured nitrogen and phosphorus in water pumped from cultivated and uncultivated plots. Nitrogen was 40–50 times and phosphorus 4–5 times greater in the water from the cultivated plot. Most of this fertilizer is contributed to the Holland River during 6 weeks in spring, and 90% of the phosphorus is in the soluble form. This large and valuable lake is undergoing rapid eutrophication, partly because of this nutrient source. But the overall contribution agricultural fertilizer is making to the nutrient loading, hence deterioration in the quality of Lake Simcoe, has not been evaluated critically.

Forestry

In many areas of Canada the forest industry has the largest single effect on the quality of the aquatic environment. The forest industry includes all phases: spraying chemical insecticides, construction of access roads, logging, soil-nutrient leaching, erosion, slash disposal, transport of logs, pulp and paper effluent, use of slimicides, mercury loss, etc. Evaluation of the impact of this industry on the aquatic environment is incomplete. This is due to several features of the industry. Logging operations are carried out mainly in areas with limited access, and then typically via company-owned roads. This results in limited public knowledge of and concern with the effect of forest practices on the environment. Secondly, the impact of logging is exceptionally difficult to measure. Gross effects may be clear enough, such as the decline in abundance of salmon in a river coincident with logging of the watershed. Translation of such gross change into an understanding of the mechanism of action has proved to be difficult. Thus, there has been only limited feedback of precautions from the guardians of the aquatic environment to the forest industry.

Access Roads

Forest access roads, at least until quite recently, were built with little regard for their impact on the environment. Such roads commonly followed streams or rivers. Reports are legion of clay banks being exposed and the endless siltation of a trout or salmon stream. The addition of this erosion material reduces the porosity of the substrate, hence its suitability for the incubation of fish eggs. Such fine material also changes the suitability of the stream for the myriad of invertebrates, especially for those in the interstices of the cobbles and gravel.

The research required here is first to evaluate the impact of road building on a variety of forest areas. Secondly, to establish guidelines for foresters and engineers for siting and construction of forest access roads. Thirdly, this concern for the aquatic environment must be included in the educational experience of foresters in training.

Logging

The immediate effect of logging is to remove the forest cover and expose the land surface to sun and rain. The loss of vegetation reduces water storage, increases impact erosion from rain, with the further loss of organic material from the soil surface. The effect then of logging is to reduce water storage on land and accelerate drainage into streams and rivers. The result is greater flooding, higher water velocities, and increased erosion of the water courses. Along the length of the stream or river there are areas of scouring and silting. Both processes are destructive of the natural habitat of aquatic organisms. Salmonid eggs are exposed and destroyed by scouring or suffocated through siltation. Rivers such as the Upper Pitt River have become much more unstable following logging of the watershed and the salmon populations have declined seriously.

One effect of removing forest cover is to permit full sunlight to fall on the water surface. Often this warms the stream to temperatures in excess of that tolerated by salmonids. The result has been the loss of trout streams, particularly in eastern Canada.

An approach to reducing the deleterious effects of logging has been to leave a band of uncut forest along the sides of major streams. Where the trees are tall and unprotected, it is common for many to be blown over by a strong wind, defeating the purpose for which they were retained.

Research directed at the effects of logging on

the aquatic environment to date has been limited. A common question is: what will be the effect of logging the watershed on the production of trout/salmon in the streams and rivers? Satisfactory predictive models are not available to estimate fish production in streams without logging, let alone after logging. Three projects have been underway to provide some understanding: one short-term (3–4 yr) in the Slim–Tumuch watershed, (Slaney et al. 1973), a second (10–15 yr) on Carnation Creek, a B.C. coastal stream (Narver 1974), and a third in the B.C. interior (Alsea River) (10–15 yr). Results of these studies, for example, in the coastal forests in Oregon, Washington, and British Columbia, are not readily transferable to other physiographic areas. Some research on coastal forest streams will have to be repeated elsewhere in Canada, notably in Quebec.

One consequence of forest harvesting, especially clear-cutting, is an increase in the amount of nitrate in stream waters (Bormann et al. 1968). This may reach levels exceeding public health standards for drinking water. Groundwater nitrate is also increased 5- to 10-fold following clear-cutting (Tamm et al. 1974). The extent to which such nutrients are leached from the soil depends on the nature of the soil and the extent of surviving plant cover. Few such studies have been conducted worldwide and almost none in Canada. A useful research effort could be mounted to establish the extent that nutrients are leached from forest soils after harvesting. Ideally this would not be limited to one soil or forest type.

Water Transport

Historically, most logs cut were moved by water. In the eastern part of the country much cutting was done in the winter and logs were floated downstream with the spring freshet. Another common practice was to construct a dam on a lake outlet to increase water storage, then blowing the dam. The large volume of water leaving the lake carried with it the mass of logs stored on the lake. These practices were extremely destructive of the stream environment, with mechanical destruction of the habitat by both logs and water. Aquatic organisms, for example, were destroyed or displaced far downstream.

Another adverse effect of logging dams was the blockage of the water course to migrating fishes. The outlet of Adams Lake, B.C., was the site of a dam that caused the extinction of a large run of salmon to the Upper Adams River. The genetic information unique to that race of sockeye has been lost and attempts at rehabilitation using other genetic stocks have not been successful. Because of such disasters, logging dams are now viewed with extreme disfavor by fisheries people, and their use generally has been greatly reduced. There are still 5000–10,000 in use in Quebec, and the effects of these need to be researched far better than has been the case to date.

Another aspect of water transport and storage of logs is the deposition of waterlogged wood and bark on the bottom. Such material may accumulate until it is many feet deep, as in portions of the Ottawa River. This organic material is rich in substances like lignin and tannin resistant to bacteria action, and breaks down very slowly. As a bottom substrate, bark is not productive of bottom-dwelling organisms and has a high oxygen demand.

Forest Insecticides

Extensive use of insecticides commenced in 1952 in New Brunswick, in an attempt to control the spruce budworm. The original insecticide, DDT, proved destructive to many nontarget organisms in the forest and streams. The killing of young Atlantic salmon, song birds, and game birds was considered unacceptable and DDT use was discontinued. In 1975 the spruce budworm was prevalent over 7 million acres of New Brunswick, 2½ million in Nova Scotia, sizeable areas of Newfoundland, Quebec, and Ontario, and parts of Maine and Manitoba. Spraying was limited to New Brunswick and Quebec using fenitrothion. These insecticides have proven to be less toxic to aquatic life and their continued use may be consistent with the recovery and enhancement of the Atlantic salmon. There is doubt, however, to the effectiveness of the spray program; after more than 2 decades of spraying, the 1975 infestation of spruce budworm was the worst to date.

One cost of the spraying program is the considerable number of man-years worked by scientists to establish the toxicity of the insecticides used, especially the toxicity for valuable species like the Atlantic salmon. Another sizeable body of expertise is involved in monitoring the environmental impact of the spray operation. The overall effect then is to commit a large body of scientific expertise to protect the salmon resource from some other human activity. With financial resources limited, such protective work is done instead of rehabilitation and enhancement of the salmon resource.

A very high priority should be given to finding an alternate, more successful method of controlling the spruce budworm.

Also of concern is the amount of insecticide lost or dumped for a host of reasons. One class of dumpings is the jettisoning of loads by spray aircraft. This occurred more than a dozen times from May 20 to June 22, 1975, in New Brunswick alone. Causes varied, some examples were: May 20, plane crashed; May 22, power loss on take-off, 625 gal fenitrothion jettisoned; May 24, bomb bay doors tripped accidentally, 625 gal fenitrothion jettisoned; May 25, 26, power loss on take-off, 625 gal fenitrothion; May 30, seventh full load lost due to failure in hydraulic lines; June 10, 10th incident, plane crashed and burned, 625 gal insecticide vaporized; June 22, jettisoned 550 gal fenitrothion at one airfield, 625 gal dimecron at another.

After the seventh incident, the EPS officer noted ". . . we can be fairly sure that the area around the Juniper airstrip is entirely free of bugs." The wonder is that it was not also free of people.

Pulp and Paper Processing

The production of pulp and paper is by one of two processes, the sulfite or the kraft process. The former is the older and involves the discard of processing water after a single use. The kraft process permits recycling of much of the process water but produces a waste, kraft liquor. The two techniques require quite different plants and cannot be converted, for example, from the older process to the newer. Generally speaking, it is difficult for old sulfite plants to meet modern effluent regulations.

A further complication is that effluents from individual plants of either type are unique in composition and toxicity. Unique, but not necessarily consistent; that is, composition varies. This variability is partly because of the large number of organic substances making up the waste. The philosophy for establishing criteria has had to be different, for example, from that in dealing with mine effluent. The latter material is defined by chemical analysis for its toxic constituents. Pulp-mill effluent is defined in terms of its biochemical oxygen demand and its toxicity to aquatic organisms. Such bioassay testing is both time consuming and costly in terms of facilities. Considerable research effort has been directed to this problem in Canada (Servizi et al. 1966; Servizi and Gordon 1972; Loch and MacLeod 1973). Effluent regulations/guidelines are now being written for the industry. Hopefully, when these guidelines have been compiled, much of this research and monitoring effort can be redirected. There are relatively few sites remaining for the construction of new pulp mills in Canada, thus the further growth of this industry may be slower in future and require less research and monitoring.

In one instance, a new kraft mill has opted for a closed-cycle system which discharges only cooling water. All processing water is recycled within the plant. The incentive for this approach is due in part to the Pollution Abatement Technology Program of Environment Canada. Hopefully this new concept will be adopted by other pulp and paper plants and other types of industries.

Slimicides, Chloralkali Bleach, and Mercury

The forest industry has had two major uses of mercury: in slimicides and in chloralkali production of bleach. In several instances the loss of mercury to the aquatic environment has been great, for example, at Dryden, Ont., and Label-Sur-Quevillon, Que.

That mercury in the environment was a problem was made clear at the 1966 Stockholm Conference. Jensen and Jernelov (1969) published the first report of aquatic organisms converting inorganic mercury to the far more toxic methylmercury. In 1970 Ontario ordered five chloralkali plants and five pulp and paper plants to reduce drastically the amount of mercury they were permitting to escape in wastewater. A joint federal–provincial law suit was launched against Dow Chemical, Sarnia, Ont., and the Lake St. Clair fishery was closed.

Mercury pollution received worldwide publicity with the report of effects on the people of Minamata, Japan. One hundred people died and 700 were blinded or crippled through eating fish contaminated with mercury. The diseased condition of the townspeople had been known for several years before mercury was identified as the causative agent.

Mercury pollution in the Dryden area, the English–Wabagoon River system, became public knowledge in 1971. Particularly affected were the residents of Grassy Narrows and Whitedog Indian Reserves, for whom the fishes of the area made up a large part of their diet. The 8000 people in the English–Wabagoon area have been urged not to consume fish from contaminated waters. Residents of the reservations have found it particularly difficult not to continue eating their traditional fish meals.

The Bell River system in Quebec appears to be even more seriously polluted. Native peoples in the area have shown high levels of blood mercury; 16 exceeded 100 ppb, 10 times the acceptable level. Three people exceeded 500 ppb, and one person 650 ppb.

There is now extensive literature on the dis-

tribution and effects of mercury (Robinson and Scott 1974; Friberg and Vostal 1972; Lambou 1972), and its persistence in the aquatic environment (Uthe et al. 1973). Several aspects remain unsatisfactory. There is still no comprehensive review of mercury in the Canadian environment. This should be prepared in the context of (a) mercury levels in waters and the fishes living therein, and (b) how much of this mercury is endemic and how much is man-made. Again it is necessary to make available the data generated in the extensive fish inspection operations. There is now enough information to make it apparent that there are areas of naturally high levels of mercury in Canada, such as Lake Evans and Lac Mistassini.

Mercury contamination, whether it is natural or man-made, has resulted in the closure of some fisheries and limited use of others. The swordfish fishery was closed in the late 1960s when Canada and the United States imposed a maximum mercury level of 0.5 parts per million. Large tuna are frequently rejected for their high mercury content; tuna slightly exceeding the limit are marketed flaked and mixed with tuna below the limit to yield an acceptable level. It is difficult to imagine how the mercury concentration in the ocean can be reduced. The only alternative approach then to utilizing these high-mercury species is reduce the mercury content of the fish tissue during processing. A research effort to this end seems warranted. This may be economically feasible for valuable species such as tuna and sword fish.

Mining

A metal mine is located at the site of an ore body, and deposits are found typically in the shield or mountain areas, that is, where bedrock is exposed. By definition such areas tend to be remote and sparsely inhabited. Historically, in the predevelopment stage, there was limited concern with the impact of such a mine on the environment. Mining companies were able to negotiate rights to pollute waters, for example, over a considerable area. As population expanded in the area of development, concern for the quality of the local environment increased, but local communities dependent on a mine/smelter for employment showed little enthusiasm for pressuring their employers to protect the quality of their environment. Pressure generated external to the community sometimes was more effective. For example, when fumes from the smelter at Trail, B.C., injured orchards in the U.S., the farmers affected complained to their government, it in turn to the government of Canada, and corrective measures were implemented. Sulfur dioxide recovery there has been exemplary ever since, partly perhaps because the recovery operation resulted in a profitable fertilizer business.

Acid Mine Waste

Many types of mining yield acid wastes. Coal mining for example may expose iron pyrite which, on oxidation, yields sulfuric acid. In areas of extensive strip mining, such as Appalachia, mine wastes have affected adversely large amounts of fresh water. To date, this has proven less of a problem in Canada. Strip mining for coal in the Minto area of New Brunswick has caused some acid pollution problems in streams draining into Grand Lake.

In metal mines, compounds of several toxic metals such as zinc and copper dissolve in acid water. Lead sulfide, for example, is relatively insoluble (Hawley 1972a), but the effect of acid waste may be to put into solution what were the insoluble salts of potentially toxic heavy metals, and make them available in aquatic ecosystems.

One of the worst causes of acid mine waste destroying a valuable fishery resource is the Brunswick #6 mine (Cook and Hoos 1971). The wastewater had the incredible composition of pH 3.0, zinc 389 ppm, copper 31 ppm, and iron 131 ppm (Montreal Engineering 1972). Fish were killed for 3 years before water quality improved sufficiently to permit survival. The Little River, where the old Brunswick #12 mine was located, plus the still-operating mill, is also heavily polluted and is reported to have no fish life in it downstream from the site. The Miramichi River has been monitored for 12 years for copper and zinc (Carson 1974), following the observation of Schofield of the downstream movement of fishes, and that of Sprague (1964), that this correlated with the high concentration of metal ions from pumping out pits and shafts.

Attempts at treating acid mine wastes have met with some success. The abandoned Wedge mine was limed last year while the search continues for a permanent solution. In this instance the company owning the mine is both large and active. No mechanism yet exists for dealing with abandoned mine contamination when the mining company has ceased to exist. Rehabilitation problems have been received by Herricks and Cairns (1973).

Of particular relevance is the work done in Canada on the role of chelating agents in binding toxic heavy metals, and the effect of alkalinity on the availability of metal ions. Especially noteworthy are the contributions of Sprague (1964), Zitko (1970), Wildish et al. (1971), Cook et al.

(1971), Cook and Côté (1972), and Chau (1973).

Mining and Processing Wastewater

Mine wastewater results from water used in the mining operation, from the entry of groundwater into mines and through the accumulation of surface water in open-pit mines. The volumes involved tend not to be very large, but the quality of such water may be affected greatly. Water from the Heath Steele mine (N.B.) has 39 ppm lead and 220 ppm zinc (Montreal Engineering 1972). This incredible toxicity was reduced experimentally by liming (Wells et al. 1974). The Giant mine (NWT) has a wastewater with turbidity of >1000 ppm and arsenic of 176 ppm (Falk et al. 1973). Clarke (1974) noted ammonia, originating from the ammonium nitrate explosives, ranged from 0.2 to 100 ppm.

Processing of minerals requires large quantities of water, an average of 800 gal per ton of ore milled in Ontario (Hawley 1973). The composition of processing water is altered by the addition of a variety of chemicals to enhance or inhibit frothing and flotation, to regulate pH, disperse slime, to act as collectors, etc. These have been documented in terms of their toxicity (Hawley 1972b). Most mills recover and recycle processing water, with some loss and makeup on each cycle. The quality of the final discharge water will vary greatly between mills, depending on the minerals mined and the extraction process in use. The Con mine (N.W.T.) has a discharge water with a hardness of 3065 ppm, chloride 3135 ppm, and arsenic of 6.8 ppm. The Giant mine's wastewater has 8.3 ppm of copper and 15 ppm of arsenic. Organic reagents added to processing water appear in mill discharge in low concentrations; xanthates 0.2–0.4 and dithiophosphate 1.2–10.0 ppm (Montreal Engineering 1972) and Kjeldahl nitrogen 1.3–12.2 ppm (Falk et al. 1973).

Mine Tailings

A common by-product of mining or milling operations is the tailings pond, a settling basin intended to trap particulate matter down to the size of rock flour. The effectiveness of such installations is variable when operational, and these structures are prone to failure when stressed by flooding. The result is the sudden release of large amounts of mine waste into lake or stream environments. For example, two breaches in tailing dykes at the Anvil Mine, Yukon, Mar. 19, 1975, released 162.6 million gal of tailings and decant (toxic and alkaline, pH 10.7). The Pine Point Mine has a tailings pond, but during spring runoff, as much as 50% of discharge passed around the end of the dyke, thus by-passing the decant system (Stein and Miller 1972). These "accidents" are environmental disasters of the first rank. A research effort to design far more "foolproof" tailings ponds is warranted.

However unsatisfactory the tailings pond may be, it is still an improvement over the direct dumping of tailings into the aquatic environment. The most incredible case must be the Reserve Mining Company's (Minnesota) dumping of 67,000 tons of tailings daily into Lake Superior. This has been going on for 19 years (Anon. 1973a, b). This is more than 5 times all the solids entering this lake naturally through shore erosion and transported via the 200 plus rivers entering the lake (Carter 1974). These tailings have now altered, esthetically and ecologically, some 2000 square miles of the lake. Communities at the west end of the lake are obliged to find alternate water supplies. It is inconceivable that Lake Superior, containing $\frac{1}{12}$ of all fresh water on this planet, could have been treated this way. There are two lessons to be learned from this outrage. One is that Canada cannot permit the despoiling of boundary waters to go on for 19 years without registering a formal complaint with the government of the United States. Secondly, Canadians cannot assume that a problem of this kind will immediately be solved by our American neighbors. (This case has been before the courts for 7 years.) Canadians will have to take a greater interest in the abuse of waters common to the two countries. The Boundary Waters Act requires that both countries do nothing to common waters that will lessen their value to the other country. Surely this covenant has been violated in the case of Lake Superior.

Within Canada, lake disposal of tailings is rare. Examples are Wabuch Lake, Labrador, and Benson Lake (Kussat et al. 1972) where lake disposal has now ceased (Hallam et al. 1974).

Air Pollution, Fallout, and Precipitation

Smelting operations may release large quantities of sulfur dioxide and considerable quantities of metals into the atmosphere. Such material is denser than air and the heavier particles appear as fallout in the vicinity of the source. Downdrafts may result in intense local fumigations at ground level. Finally all atmospheric contaminants may be carried back to earth by rain or snow.

Historically, smelting of sulfide ores consisted of roasting, that is, oxidation that yielded sulfur

dioxide. For example, in the Sudbury area commencing in 1885 nickel ores were roasted in the open and the fumes destroyed plant life for miles around. (Nineteen eighty-five will mark 100 years that people have been complaining about air pollution in the Sudbury area.)

In certain localities the amount of sulfur dioxide so released may be very large and influence greatly the aquatic environment for some distance. Smelters in the Sudbury area, for decades prior to the closing of Coniston and erection of superstack, released some 2.6 million tons of SO_2 annually. This gas, a precursor for sulfuric acid, is very soluble in water and is returned to earth as acid rain or snow. The effect on the aquatic environment is the acidification of lakes and streams (Gorham and Gordon 1960; Beamish and Harvey 1972). Changes in the biota may be great, with the loss of some or all species of fishes (Beamish 1974; Harvey 1975a; Beamish et al. 1975) and unusual zooplankton communities (Sprules 1975). Other point sources of sulfur dioxide release are having a similar effect elsewhere, such as the sintering plant at Wawa, Ont. (Gordon and Gorham 1963).

The problem of acid precipitation and its effects on fresh waters is not limited to the region of point sources of SO_2 release. The phenomenon has been recognized for many years in Scandinavia. The southern portion of Norway and Sweden receives large amounts of acid precipitation originating in western Europe from burning sulfur-bearing coal and vehicle exhausts (Anon 1972; Willen 1972; Odén and Ahl 1975). If this acid precipitation continues, most fresh waters in the southern quarter of Sweden and Norway will be so acidic as to be inhospitable to desirable species of fishes by the turn of the century.

Recognition of this broader problem has been slow in coming in North America. The impact has yet to be defined of the industrial and domestic pollutants emanating from Detroit, Chicago, Cleveland, Toronto, etc., on the lakes of Ontario. That this industrial belt is affecting the lakes in New York State has been reported (Adirondack League Club 1971; Likens et al. 1972). The need in Canada is for a transdisciplinary study of the problem, where the effect on fresh water, hence the biota, would be but one (albeit important) component.

The first attempts (1973) have been made at reclaiming acid lakes in the Sudbury area (Adamski and Michalski 1975; Schneider et al. 1975). These workers reported on the chemical changes in two lakes following treatment with lime or lime plus calcium carbonate. The following year Hannah Lake was treated with calcium hydroxide and calcium carbonate. The intent was to treat Nelson and Joe lakes in 1975. The further intent is to stock these lakes with fish and create a sport fishery to replace that lost during acidification. What is not known at this time is what species of fish will now flourish in these twice-altered environments. That is, what are the water requirements of fishes in relation to these artificial environments.

Terrestrial vegetation levels of sulfur, arsenic, copper, iron, nickel, and selenium were elevated (Water Pollution Control 1973; Costescu and Hutchinson 1972) especially northeast of Sudbury. Lakes in the area have abnormally high levels of heavy metals, especially copper and nickel, and the limited algal flora is adapted to these high concentrations (Stokes et al. 1973).

Power Generation

Early in the settlement of Canada it was recognized that water power to drive the grist mills and saws of the pioneer economy was available at relatively low cost. Old dams and mills still dot the landscape of eastern Canada. Their effect on the environment, such as impounding a stream into a pond or lake, usually was small. The many dams on rivers such as the Credit, Humber, and Don (north shore of Lake Ontario) undoubtedly contributed to the loss of Atlantic salmon from these streams.

Hydroelectric Dams

Electrification in Canada began late in the 19th century; for example, the first hydraulic generating plant in Ontario was probably that of the Ottawa Electric Light Company in 1881, lighting a lumber mill. Less than a century later there remain few hydroelectric power sites in settled Canada. There is still a sizeable potential in Labrador, in the Quebec portion of the James Bay drainage, on the Nelson River in Manitoba, and on several rivers in British Columbia. Much of this potential development currently is in planning or construction stages. Relative to the total installed generating capacity in Canada and that under construction, there remains little potential for further hydro development, outside of Labrador and British Columbia.

The environmental problems associated with hydro development have been researched intensively in Canada, perhaps better than anywhere else. This work has been collated into several thorough reviews (Andrew and Geen 1960; Geen 1974; Efford 1975; Efford and Smith 1972). The problems associated with dam construction are

many, and several are particularly difficult to research. One of the most intensively studied is that of fish movement and distribution in the reservoir created behind a dam. Both upstream and downstream movement of salmonids is slower, and the fish may become lost. Passing fish by an obstruction such as a dam presents problems of collecting or concentrating the animals at one location, the entrance to a fishway or a transport chamber. Many schemes have been proposed to achieve this with only limited success.

A dam can create a number of other changes in the quality of the aquatic environment. The surface waters of the reservoir may warm to the extent that salmonids will descend to cooler depths. This activity may preclude their downstream escape from the reservoir if the only exit is at the surface. A serious problem on the Columbia River is supersaturation of the entire river with nitrogen, as a consequence of spillway water carrying entrained air to depth and additional gas entering solution under pressure (Harvey 1975b). Another problem is the change in the chemical nature of the water as a consequence of creating a reservoir from a lake or river. Those chemical cues used in fish navigation may be lost.

A considerable body of expertise with experience in researching these problems exists in Canada. Fisheries agencies (provincial, federal, and international in British Columbia in particular) have researched many problems. In general, the policy of provincial and federal governments is that salmon rivers will not be used for power generation. If that policy is reversed in future, new research initiatives would be necessary.

There remains another group of problems associated with hydroelectric development that have been inadequately researched. This is the extremely poor or nonexistent follow-up that accompanied dam construction. Most dams have been built with no preconstruction assessment of environmental change. Thus, we have no knowledge of the effects of the dams on the St. Lawrence River and their possible role in the loss of important fisheries such as sturgeon and striped bass. The recent work of Sutcliffe is unnerving. It would appear that the rivers entering the Gulf of St. Lawrence are the force that drive the circulation of that great and productive water body. Impounding the rivers, thus controlling their spring discharge, profoundly reduced the upwelling of nutrient-rich waters.

Another underresearched problem is the quality of the aquatic environment produced in a reservoir in the sense of productivity. Flooding a river valley initially results in the leaching out of nutrients into the water body and increased biological productivity. This increase tends to be short-lived and fish populations fall to or below their preimpounded level. Proposals for creating reservoirs often contain sections dealing with the new fishery that will be produced with the creation or enlargement of the water body. One is hard-pressed to find an instance in Canada where these anticipated fisheries were realized.

Similarly, sport fisheries in reservoirs have limited popularity. The recreational experience is marred by the innumerable protuding dead trees and by mud flats when the reservoir is drawn down. The gradual destruction of such drowned forest is measured not in years but in decades or centuries.

Impact assessment statements for new dams is a recent innovation in Canada. None was made for the Churchill Falls, Labrador, development, and none was made for the James Bay project, prior to the beginning of construction. Detailed basin studies have now been prepared in connection with the impoundment of the Churchill River, Saskatchewan, and the diversion of the Churchill River into the Nelson River, Manitoba. Smaller studies have been conducted on other rivers, e.g. Snare River, N.W.T. (Weagle and Cameron 1974). It is proposed that South Indian Lake be studied postflooding; if this is done it will be the first evaluation of the environmental impact assessment process for dams and reservoirs. That is, for the first time we will have a measure of accuracy of an assessment. Current ecological concern would force assessment of any additional impounding of B.C. rivers, and hopefully this concern will operate at the remaining dam sites in Labrador.

With the period of expansion in hydroelectric power generation rapidly drawing to a close, it is difficult to see any great need for research initiatives in this area. What damage has been done is done and cannot be undone by a better understanding of the way it happened. Sufficient manpower is available to deal with the modest future expansion of hydroelectric development. Although the data base is weak, it is probably adequate to meet the limited needs of the future.

Fossil Fuel Plants

In the absence of adequate hydro power, historically and still the commonest method of producing electricity has been through burning coal, oil, or gas. The steam produced drives turbines, is condensed, and the waste heat is carried away in cooling water. Such plants have a low efficiency and the amount of heat jettisoned into the envi-

ronment is very great in large plants. Adequate cooling water becomes the first consideration in locating such a plant on a river, lake, or ocean coast. Where water is in too short supply for oncethrough cooling, heat loss may be through evaporation of a smaller amount of water. One advantage of fossil fuel plants is that they can be started up and shut down rather quickly. They are thus particularly well suited to provide peaking-power, with sudden increases or decreases in heat lost, hence the temperature of the cooling water.

The environmental impacts of such plants are many, and have been researched thoroughly in the eastern U.S., especially at plants on the Ohio River within the Tennessee Valley Authority and on the Great Lakes. One effect is the physical attraction of fish to areas of current or warmer water. Typically fish must be kept away mechanically from cooling water intakes and sometimes from the heated water discharge. Cooling water temperature is usually raised 10–20 C and may exceed the upper lethal limit for some or all species, especially in summer. In winter, fish acclimated to warm cooling-water may be suddenly exposed to much lower temperature when a plant is shut down. Sizeable kills of fish have resulted.

Another consequence of heating water is a reduction in its capacity to hold dissolved oxygen. The fish is in the difficult position of increased metabolic activity through elevated temperature and reduced oxygen content with which to meet it. The result may be a reduction in the scope of the animal for additional activity. Over the short term, heating water reduces its capacity to hold nitrogen but gas may not be lost. The resulting supersaturation may cause gas disease (Harvey 1975b) and the death of the animals.

Waste products of fossil fuel burning are a problem. Sulfur-containing coal, oil, and gas yield large quantities of sulfur dioxide that returns to earth as acid precipitation. The extent and the seriousness of this phenomenon is only now being assessed in North America, but the total research effort is still small. Much of the science basic to the problem described above was pioneered in Canada and there exists again an adequate research base both in expertise and information. Much of this base is the work of F. E. J. Fry and his students (Kerr and Lawrie 1976).

Nuclear Reactors

The first commercial production of electricity by nuclear reactor began in Canada in 1962 with the experimental reactor NPD at Rolphton generating 25,000 kw into the Ontario grid. An experimental reactor WR-1 began operating in 1965 at the Whiteshell Nuclear Research Establishment. This unit uses light oil as the medium for heat transport, and the 60,000 kw of heat produced is dissipated into the Winnipeg River. This was followed by the Atomic Energy of Canada Limited (AECL) Candu design at Douglas Point, that came on line with 200,000 kw in 1967. A boiling light water reactor (BLW) was built by AECL and operated by Hydro-Quebec, coming on line in 1970 with a power production of 250,000 kw. The Pickering generating station was built by Ontario Hydro and when the first of four reactors came on line in 1971 it became the world's largest at 2,160,000 kw. Currently under construction is Bruce generating station with four reactors entering service 1976–78 for a total capacity of 3,200,000 kw. Also under construction by Ontario Hydro is Pickering B, which will double the power production of the present station, 1980–82. A reactor generating 3 million kw, sited at Bowmanville will come on line 1981–83 (Ontario Hydro 1974). The next nuclear generating station, to be sited in the North Channel region of Georgian Bay, is in the planning and public discussion stage. The first reactor in the Maritime Provinces is under construction at Point Lepreau, N.B., a single reactor with a power output of 500,000 kw.

It is not clear how soon this rapid expansion of nuclear power in Ontario will be repeated in other provinces. Over the short-term, Newfoundland–Labrador, Quebec, and Manitoba will receive large amounts of hydro power from projects planned or under construction. Alberta and British Columbia have declared for coal-fired plants for the immediate future. Nuclear generating capacity has been predicted for Canada for the next few decades and clearly this is the energy source to which all provinces must turn. It is also germane in such predictions to have regard for increased use of electricity as supplies of fossil fuels diminish. To replace, for example, the natural gas currently consumed with electrically produced hydrogen, would require doubling the currently installed generating capacity.

Nuclear reactors require enormous volumes of cooling water. Pickering pumps a million gallons a minute and the filtering screens serve as a remarkable trap for fishes, especially alewives. Daily "catches" of 30–60 ft^3 are common, 100–200 occasional and as much as 400 ft^3 has been reported. No use has been found for this material and ways of avoiding the collection of these fish are being explored.

The shift in technology of power production

contains both old and new problems of environmental quality. The problem of jettisoning large amounts of heat is common to the use of fossil fuels. For the present at least, this heat loss in so cold a climate as Canada has not created many environmental problems. Also, there is a growing appreciation that this heat may yet have some value. At both Point Lepreau and Pickering, studies are underway to determine the usefulness of such heated water in fish culture. Baie du Doré (Douglas Point) studies have been conducted on the effect of warmer water temperatures on small mouth bass, particularly in the context of spawning and growth.

The greatest concern is for the loss of radioactive material into the aquatic environment. Reactors, of course, are designed to prevent this. The Candu heavy-water design in particular makes such contamination extremely difficult. Heavy water per se is not a hazard but tritiated heavy water is formed during neutron bombardment within the reactor. This material is a beta emitter, penetrates the skin readily, and has a half-life of about 12 years. Emery (1972) reviewed the concern for radioactive contamination of the environment.

The expertise for monitoring radioactivity in the Canadian environment is good to excellent. National Health and Welfare, AECL, Ontario Hydro, and Hydro-Québec are all involved. Health and Welfare Canada carries the primary responsibility for public health, AECL for determining background levels throughout the country and monitoring their own activities, and provincial hydros monitor in a wide area around their facilities. These monitoring responsibilities are entrusted to highly trained people. Technology of monitoring is at a high level of development, is easy to calibrate, and highly reproducible. It is probably undesirable that virtually all expertise in this field is governmental, federal and provincial. This results in an unusual amount of secrecy and with less of the checks and balances in the form a body of expertise outside government, than is the case in other segments of society.

Some problems associated with nuclear reactors remain. One is the fate of spent fuel rods permitted to accumulate for a few decades. This waste material contains some 250 materials, and more than half, including plutonium, are radioactive. The intent is to process this "waste" into usable fuel, but this material is extremely difficult to handle. As the technology for transporting and processing the material is developed, it will have to be subjected to the closest scrutiny with respect to the loss of these hazardous substances into the environment.

A more serious problem with light-water reactors is the amount of trace-element material that escapes from the reactor. In the Candu reactor this loss is minimal and is less than the amount of trace elements liberated in burning soft coal. The extent of the build-up of trace elements in aquatic environments in particular; and the biosphere in general, is inadequately documented. It is essential to know the extent that such material accumulates in living systems and is multiplied in passing up the food chain. In the case of P^{32}, for example, this increase from environment to top consumer is one million-fold.

Transportation

This industry, including road, rail, air, water, and pipeline transport creates a variety of problems in the aquatic environment. These result from the loss of product, from waste disposal, and from special treatments/processes used in the industry.

Shipping

The dominant environmental concern in ocean shipping is the loss of petroleum. Tankers are lost each year from a variety of causes, including human error. The *Torrey Canyon*, for example, struck the best charted rocks in the world. "Accidents" such as this cannot be legislated against. Nor have punitive levels of fines or insurance rates had much effect.

The next level of concern is the loss of oil from tankers washing out bilges at sea. By law, this is to be done not less than 50 miles at sea and oil is to be released at a prescribed rate of so much per mile. In practice this is violated. A supertanker for example jettisoned an estimated 100,000 gallons of crude oil within a few miles of the coast of Florida, August 1975. This combination of accidental spills and bilge cleaning results in a perpetual oil slick on the waters of major Canadian harbors.

Occasionally other products are lost in loading/unloading or at sea. They may attract considerable publicity, as for example in the search for the tank cars of chlorine lost from a barge in the Strait of Georgia. Few instances are recorded where products other than petroleum have been lost in Canadian coastal waters and caused environmental damage.

Ontario currently has a law that requires pleasure craft to have pump-out tanks for holding sewage wastes for subsequent on-land disposal. No parallel legislation is in force for the U.S. half of the four international Great Lakes. Nor is

there any requirement that ocean-going vessels entering the St. Lawrence Great Lakes hold waste for disposal on land or at sea. Vessel transits exceed 6000 annually on the Great Lakes. Most Great Lakes cargoes are bulk, consisting of ore, coal, grains, and limestone; that is, relatively nontoxic materials. The *Edmund Fitzgerald* for example, sank in Lake Superior, Nov. 10, 1975, with a cargo of 26,116 long tons of taconite. Presumably, the 75,000 gal bunker C oil on board was lost to the environment. Since the oil shortage, petroleum shipments on the Great Lakes have risen and now exceed 5 million tons annually. The loss of a tanker the size of the ore carrier *Edmund Fitzgerald* anywhere in the St. Lawrence seaway will constitute an ecological disaster of the first magnitude. The principal concern in Great Lakes shipping must remain the accidental loss of hazardous chemicals. Recalling the disasters caused on the Rhine from the loss of a single barrel of insecticide, there is good reason for concern.

Highways

There are multiple daily accident reports filed by EPS describing the environmental contamination from lost products. The majority are petroleum spills and a small number involve hazardous chemicals. Shipment of hazardous chemicals, including the types of containers, is covered in good legislation, but this cannot prevent a vehicle from leaving the road and losing part or all of its cargo.

A different type of problem is the application of chemicals to roads; salt, calcium chloride, oil, urea, etc. Road salt, for example, is used heavily in eastern Canada and locally has had considerable effect. Some small lakes in Newfoundland show total dissolved solids raised from 50 ppm in summer, to 200 ppm in winter. The sodium chloride content of the lower Great Lakes has more than doubled in the last few decades, and this must be attributed in part to the use of road salt.

Railroads

Historically railroads have taken the attitude that their rights-of-way were sacrosanct. The railroads were not answerable to anyone for what they did along their tracks. Thus, trains discharged sewage directly onto the road bed. Had bus companies tried the same approach, they would have been treated as lunatics.

Derailments and associated loss of material tend to be greater environmental hazards than road spills. This is due to the greater quantity of the material, the tendency to ship hazardous materials by rail, and the often greater difficulty of access for cleanup.

Pipelines

Pipeline breaks have attracted remarkably little attention. These occur in Alberta, for example, at an average rate between one and two per day, and may reach five or six daily. The cause is commonly a shift in soil masses. Cleanup of oil spills typically takes the form of burning the liquid waste and plowing the oil-impregnated soil. Natural gas leaks can be almost as messy, with liquid condensates and sulfur accumulating at the break. In a few instances pipeline breaks in close proximity to water have contaminated aquatic ecosystems. There are few published reports evaluating such impacts. Petroleum spills, exclusive of pipeline breaks, are very nearly a daily occurrence in the range of 100–1000 gal. Even more disturbing is the frequency of larger spills (Table 3).

A related problem is the loss of petroleum products into ground water. More than 500 wells in Canada are contaminated in this way. The cause is typically a leaking storage tank in a service station or furnace oil tank. Such contamination is relatively long-lived and has received limited study. The current method of disposal of "waste" petroleum is typically to dump it on the ground. This may contribute to groundwater contamination in some areas.

Petroleum products in water may contaminate fish to the extent that it is unfit for consumption. This is a problem, for example, in mullet from parts of Moreton Bay, Queensland, Australia. A point-source of this contamination has never been found. The cause may be the sum total of all petroleum wastes entering the Brisbane River. That is, street oil, service station wastes, car wash wastes, and such like. A few instances of "phenol" taste have occurred in fish from inland lakes. Lake Winnipeg would be especially susceptible to this. Some sport fisheries have also suffered from this, such as the Bow River downstream from Calgary, and the North Saskatchewan River. Storm sewer waters may account for a significant portion of this contaminant.

Recreation

Recreation is one of the largest uses made of the aquatic environment in Canada. Generally speaking, recreation requires that environment be of high quality, in the sense of unaltered by human activity. People want to drink, swim in, travel on, dive in, and fish in clear water with

TABLE 3. Selected examples of large petroleum spills, first half of 1975. (Source: Environmental Protection Service)

	Volume (*gal*)	Type	Site
Jan. 19	10,000	Bunker C	Sunoco, Que.
Feb. 10	50,000	Bunker C	Air Canada, Que.
Apr. 7	18,000	Diesel fuel	WPYR, Yukon
Apr. 14	19,285	Gasoline	Imperial, N.B.
May 2	1,000	Gasoline	WPYR, Yukon
May 3	8,000	Cutting oil	Barton Tubes, Ont.
May 3	1,025	Gasoline	Imperial, N.B.
May 8	1,500	Diesel fuel	Golden Eagle, Nfld.
May 11	16,000	Furnace oil	Ouimet Gobeille, Que.
May 22	10,000	Bunker C	Mt. Sinai Hosp., Que.
June 5	30,000	Diesel fuel	Cantung Mine, N.W.T.
July 3	3,000	Bunker C	CNR, N.B.

low levels of disease-causing organisms. Because of this recreational requirement of a high environmental quality, recreation tends to be in conflict with almost every other use of the environment. For example, along the eastern slopes of the Rockies, the streams are the natural foci for summer recreation. Competing, and at times mutually exclusive, uses for this area are: strip-mining for coal, oil and gas exploration, logging, cattle ranching, irrigation water demands, and feed lots.

NATURE OF RECREATION

The total recreational experience cannot be defined in simple terms. The components vary between individuals, and many substitutions in terms of rewards or satisfactions are possible. Many questionnaires have been devised to establish what it is that people want in their recreation. For example, in polling sports fishermen, the act of catching a fish is well down the list of priorities, so far down that fishing is almost the activity of not catching a fish. High on the list of reasons/rewards for fishing are escape from urban crowding, solitude, peace and quiet, fresh air, etc.

If this is the case, then the quality of the aquatic environment for recreation must be viewed from the position of the person seeking recreation. For example, when the first cottage is built on a lake, the resident achieves most or all the objectives sought in the recreational experience. When the second cottage is built, solitude is lost, and more privacy is lost with each succeeding cottage. Soon there is a conflict between developer and resident. The developer seeks to maximize cottage density, hence, financial return on investment, and the residents seek to maximize their rewards by minimizing crowding. Municipal authorities tend to be more responsive to the increased tax base which accrues from development, and to opinions of year-round residents who vote locally than to summer cottage owners who do not. The tendency then is for a lake to become ringed with cottages, often to a to a density that compromises or destroys those values in recreation that attracted people to the area in the first place, The ultimate expression of this is the high density community of cottages extending back from the lake and/or high-rise apartment buildings on the shore of the lake. Such resort living may be anathema to the person who currently enjoys a view of the lake from his cottage, but for the person with no cottage now, these high-density "solutions" may be better than no cottage at all. There are now 395,195 households in Canada with one or more cottages (Statistics Canada).

ENVIRONMENTAL IMPACT

Recreational activities vary greatly in their impact on the aquatic environment. Some activities themselves have very little effect. These include canoeing, sailing, photography, diving, swimming, and nature study. These activities are the same ones, partly by definition, that tend not to spoil the recreational experience for others. Some recreational activities are competitive, such as sport fishing, in that the success of one person may reduce the success of another. There is a third class of recreational activities which tends to be more demanding of the environment and for various reasons may reduce the quality of the recreational experience for others. These include power boating, water skiing, snowmobiling, waterfowl hunting, etc. The actual physical dam-

age to the environment by these activities tends to be small. Lake pollution from outboard fuel has been the subject of several studies and usually no effect could be detected. The effect of the snowmobile has been to extend greatly the territory available for winter recreation. This new mobility in winter has resulted in greater resource use, especially through ice fishing. R. Ryder's observation of a group of anglers harvesting from a lake (accessed by snowmobile) 2 years' production of lake trout in a single day is an alarming one.

There is a need for a better understanding of the value judgments people make in their choice of water-based recreation. Several good attempts have been made at placing a dollar value, for example, on fishing recreation (Sewell and Rostron 1970; Pearse and Laub 1971; British Columbia Fish Wildlife Branch 1971). It would be useful if a group of social scientists could now analyze recreation, identifying and quantifying the experience in terms other than dollars.

Another measurement better left to the social scientists, is how much success at fishing is necessary to maintain the pastime. Obviously this differs between individuals, within the same person over time, and with the "value" of the species pursued. At the present time the quality of sport fishing is measured in part by the kinds and amounts of fish caught. People charged with providing this recreation have little in the way of guidance as to how much is reasonable, adequate, or plush. As a minimum it would be useful, in the face of ever-increasing cottage development, to be able to advise people of the minimum and maximum levels of fishing success they could expect for a given level of development.

Cottage Density

The greatest effect on the environment by recreation is the construction and use of accommodation and other facilities on the lake shore. In a typical scenario the first effect is that of clear-cutting the construction site, and often beyond the site. This is followed by the provision of some form of sewage disposal; direct flow into the lake at worst or disposal field/pump-out tanks at best. Thereafter follows the construction of a dock with the necessary modification of the inshore habitat. The desire to swim close inshore requires that the aquatic vegetation be reclassified "weeds" and removed. To create a beach, sand may be dumped on the more productive substrate. Where "necessary," wetlands are drained and shallows filled in. This is repeated with each cottage builder. Soon the second phase begins: "The lake isn't like it used to be" phase. Loons, herons, and blackbirds are seldom seen; pike and bass fishing deteriorates. The cottagers refuse to associate their activities with the destruction of the aquatic environment and the reduction in these species. It is assumed that everyone can remove the weedy habitat of the bass and drain the spawning areas of the pike without these populations being affected. In the popular jargon, the lakes are simply "fished out."

The growth or expansion of cottage development is still in progress. In Ontario for example, the Ministry of Treasury, Economics and Intergovernmental Affairs has to vet some 11,000 individual requests for land severance for cottage lots annually. In addition, there are developer's type of requests for cottage development on larger tracts of land. During this period of cottage development many problems remain inadequately answered. For example, provincial and municipal officials lack simple, management-oriented models to predict environmental degradation over a range of intensity of development. The first stages of this have been done (Hough Stanbury and Associates 1972; Lakeshore Capacity Study 1974).

A separate model for nutrient loading in relation to cottage development could be very useful to planners and custodians of environmental quality. Such a model would have to be very reliable, with the capability of accurate prediction, and defensible in a court of law. That is to say, were such a model invoked to establish an upper limit on the number of cottages permitted on a lake, it would immediately be challenged, in the context of "Demonstrate that the aquatic environment cannot tolerate even one more cottage." There is now sufficient information to produce such first-generation models and some have appeared.

The bases for such models are the relation between chlorophyll and nitrogen and phosphorus. Sawyer (1947) indicated excessive algal growth would not take place if these nutrients were prevented from reaching defined critical levels. In a logarithmic plot, Sakamoto (1966) presented a linear relation between total phosphorus in spring and summer concentrations of chlorophyll. A model to determine a lake's trophic state was developed by Vollenweider (1968) based on phosphorus loading and mean depth. This attempt was followed (Vollenweider 1969) by a model correcting for flushing rate and sedimentation. Dillon (1974) calculated the inflow of nutrients from a series of lake basins, and Dillon and Kirchner (1975) corrected this for forest cover vs. forest plus pasture.

At least three attempts have been made to apply variations of the above approaches to predict cottage capacity of lakes. Michalski and Conroy (1972) developed a system for classifying lakes by water quality, including attributes important to fishes. Shannon and Brezonik (1972) established critical and allowable loadings of phosphorus for a large group of lakes in Florida. These values may be too high for lakes in Canada. Hutchinson et al. (1973) suggested an approach for modeling nutrients, hence trophic status in relation to cottage development. Dillon and Rigler (1975) presented a model which compares nutrient loading with four arbitrary ranges of chlorophyll concentration. This would permit the planner/manager to categorize a lake and then add cottages until increasing nutrient loading threatened to push the lake into the next trophic category. The cardinal weakness in all these models is the arbitrariness of making a yes–no response (develop more cottages or don't) along a continuous spectrum of nutrient loading. This arbitrariness is unsatisfactory in that it is difficult to defend by the custodian of environmental quality and may not prove useful in law.

There is still a poor understanding of how much nutrient is contributed to a lake via septic disposal systems. Estimates range from all to none. Septic fields located on bedrock have little effect even in delaying the flow of nutrients into a nearby lake. Deep soils, for example at the main camp, ELA Lakes, appear to be trapping all nutrients. Again a model, even a complex one, would be helpful in siting cottages to minimize the flow of nitrogen and phosphorus into the lake.

Finally, there is a need for a further look ahead, a decade and more. Water-based recreation is often energy intensive, with large amounts of petroleum consumed in travel to and from the site, heating the additional dwelling, and in power boating and snowmobiling as activities at the recreational site. What is the fate of such wilderness recreation when petroleum fuels become too scarce/costly to be used for this purpose? In short, what is the role of the aquatic environment in providing recreation in the Conserver Society?

Conclusions

1. Despite the clear repudiation by Bruce and Maasland (1968) of the concept of unlimited fresh water, Canadian attitudes and policies still overestimate both the quantity and quality of this resource in Canada. The temptation was great to entitle this report after the words of F. E. J. Fry: "The great Canadian fallacy — half the world's fresh water."

2. Water quality problems across the country are highly specific to regions. This is further complicated by the diverse stands taken by provincial governments. The attitudes taken by the provinces vary, for example, whether they are headwater provinces, like British Columbia or Alberta, or lowlands like Manitoba. In the cases of the former, they feel little need for a federal presence; in the latter case, only the federal government can protect it from polluted waters entering from the east, west, and south.

3. The greatest effort in pollution control by both federal and provincial organizations, has been in the area of point-source contamination of water. With few exceptions, monitoring and the research base are adequate. In some areas, the effort may be excessive. In contrast, nonpoint sources of aquatic environmental degradation are underresearched and less adequately monitored.

4. Research capability varies greatly between subdisciplines. Where strong schools have emerged, such as in fish physiology, there is a plethora of expertise across the country; or where there has been a major federal research effort, such as chemical monitoring of water quality. Concurrently, there are several areas of serious weakness. The modest body of expertise is inadequate to interpret the water quality data. Remarkably little use is made of indicator species in defining environmental quality; expertise is scant and the research base small.

5. There is a remarkable paucity of innovation in research on freshwater environments. The literature abounds with mathematical models and indices developed outside Canada. Few new approaches, either in technique, economy of effort, or interpretation have been developed in Canada. Three disciplines dominate work on the aquatic environment: water flow, water chemistry, and fish physiology/toxicology. This has its origins in the disciplines of the workers (engineering, chemistry, biology) and is formalized in the mandates of the principle agencies (Inland Waters Directorate; Fisheries Management Service). No mere intradepartmental committee in Environment Canada can bridge these paradigmal and administrative chasms.

6. Compared with that of the federal government, the research contribution of the university sector is now modest and becoming smaller. Financial support for universities through the National Research Council of Canada was frozen

in 1969 and inflation subsequently has reduced the value by more than 40%. Relatively little of the NRC expenditures, perhaps a fifth of 1%, are for 18 grants in aid of research on aquatic environmental quality. The Fisheries and Marine Service grants one-third of a million and Inland Waters Directorate one million dollars annually and some of the monies are for research on aquatic environmental quality. These modest levels of financial support largely determine the effectiveness of the university sector to contribute research and trained personnel in the area of the aquatic environment.

7. Specific governmental initiatives have helped enormously to identify and rationalize regional environmental problems. Most notable are the transdisciplinary basin studies, conducted under federal–provincial agreements, and through the initiative of Inland Waters Directorate. In general, studies on this scale have important goals, are well planned, have clear operational direction, and are adequately financed. The role of small-scale or artisanal science in the achievement of broad environmental objectives is more difficult to define and the value harder to identify; but these alone are not grounds for abandonment.

8. Tragically, the federal government and most provinces have gone their separate ways in terms of methodology of water analysis and the associated data storage base. The various systems are largely incompatible. The Canada Centre for Inland Waters has taken the initiative in evaluating the chemical methods in use across the country, and in that way at least data can be compared.

9. Bruce and Maasland (1968) identified the need for a Canadian scientific periodical dealing with all aspects of water. *The Journal of the Fisheries Research Board of Canada* most closely meets this need.

10. The library service, both within Environment Canada and for science generally, is excellent. Information searches through CAN-OLE and WATDOC provide researchers with extraordinary support.

11. It should be remembered that the large effort and expenditure needed for protection of the aquatic environment is the result of demophoric growth (as defined by Vallentyne 1972). Relatively little effort is expended on research into that root cause. Furthermore, resources expended in protection do not necessarily enhance the species or environment protected. It would be relatively easy to devote all financial and manpower resources to protection at the expense of understanding and meeting the food needs of indigenous peoples, enhancement of Atlantic and Pacific salmon, research on the culturing of scallops and lobster, etc.

Recommendations

Monitoring

1. The need is not for more financial and manpower resources to protect the aquatic environment. The need is for more rational and effective use of existing resources. This can be in many ways, most notably by reducing duplication of federal–provincial effort; by reducing duplication within the federal government; by reducing secrecy in data, hence repeated effort by agencies; by reducing internecine wars between environmental agencies; by more critical review of research, travel, and office expenditures. Too often restraints within the government service are perceived as financial and/or manpower when the root problem is ethical, legislative, territorial, or administrative.

2. The total effort devoted to monitoring pollution in the aquatic environment is not well balanced. The current effort is adequate to excessive in the area of point-source contamination. Diffuse sources of pollution have been largely neglected and warrant a larger effort.

3. There remains a considerable duplication of federal and provincial effort, especially in the area of pollution monitoring. More of this responsibility could be given to the provinces, and the federal effort redirected.

4. One of the first lines of defense in avoiding a mercury-type crisis is the Fish Inspection Branch. Considerable secrecy surrounds the data gathered and the interpretation done on this data. Openness in both respects could only enhance the effectiveness of the surveillance. It would also result in a reduction in duplication of this effort by other agencies needing the same data.

5. A disproportionately large effort is devoted to monitoring water chemistry and fish physiology/toxicology and this could be reduced. The effort expended on ecosystem approaches is small and should be increased.

6. A large effort is being expended on gathering data that are not fully analyzed or used. The interpretation of water chemistry data is especially weak and should be given a higher priority.

7. There is excessive effort applied to the development of new chemical methods for standard testing. Federal laboratories and many provincial laboratories have prepared their own manuals. The incentive to develop new methods appears to have its origins at least in part, in the personal drives of the chemists. In the collection

of routine data, publication is largely restricted to new methodology. Some of this creative drive of the water chemists should be directed at data interpretation.

8. Federal and provincial agencies have adopted individual data bases, making it difficult to share data and interpretation. Over the long term, an effort should be made to minimize the number of bases in use.

9. Long-term monitoring of specific pollution problems warrants closer scrutiny. Some monitoring is directed at what are now nonproblems that are not expected to become problems.

RESEARCH

In general — 1. There is a need for the application of systems ecology to the management of environmental quality, with human impact assessed on the whole ecosystem.

2. There is need for a greater research effort on the usefulness of species and communities as indicators of aquatic environmental quality.

3. There is a need for strategies to reduce the amount of testing in both routine water monitoring and pollution control.

4. There is a need for innovation in environmental monitoring.

5. There is a need for research in Canada into approaches and techniques of data analysis.

6. The contribution of the university sector to research on aquatic environmental quality is small. Granting through the National Research Council of Canada with the associated academic peer–review system makes the most effective use of the limited funds available for scientific research in general. But research into specific environmental problems will have to be funded through another route. University research funding through the Department of the Environment currently is small. The role of the universities in environmental research needs to be reviewed. This should be done by a panel with good representation from outside Environment Canada.

7. Workers in different aspects of environmental monitoring such as fisheries, chemical water quality, and water quantity, have remarkably little to do with each other and make remarkably little use of each other's data. Attempts should be made to bridge these gaps, for example, through exchange of researchers working at levels ranging from data interpretation to policy assessment.

8. The current series of watershed studies sponsored by Inland Waters Directorate should be continued and extended. The approach followed could well serve as a model for other large, interdisciplinary studies on the environment.

9. At 5 years of age, Environment Canada is still a very young department. Individuals still have roots in old agencies (Fisheries, Forestry, Energy, Mines and Resources, Meteorological Service, etc.). Many units remain isolated because they are housed in separate, widely-spaced buildings. Special effort is required to get people from the various groups to research together problems that occur at the interfaces between two or more agencies. An example of such a problem would be the effect of air-borne pollutants, originating in the Detroit–Chicago–Cleveland–Toronto area, on the lakes of Ontario. The suggested model is a negotiated cost and work sharing agreement involving federal, provincial, private, and university sectors. Most importantly, the project has an identifiable goal, a beginning and an end.

10. It is not too soon to begin to identify the role of the aquatic environment in the concept of "Conserver Society," as developed by the Science Council of Canada (1973).

By economic sector — 1. Municipal waste from 23 million people is the largest environmental problem in Canada. Municipal waste includes a large portion of the total industrial wastes of the country, in that many industries, large and small, discharge into municipal sewers. The technology for dealing with this waste has changed little in the 60 years since the introduction of the activated sludge process. (a) There is a need for research on the fate of toxic substances in municipal wastes, including heavy metals, insecticides, polychlorinated biphenols, bacteria, and virus particles. Such research is equally relevant for on-land disposal and disposal in water. (b) There is a need for research on the fate of heavy metals, viruses, and bacteria where sewage sludge/effluent is employed in crop irrigation. (c) There is need for research on the level of sewage treatment required for protection of quality of the shellfish resource, and possibly the fin-fish resource. (d) There is a need for research on alternate waste treatment systems in the colder, northern areas of Canada.

2. Recreation carries with it the twin problems of the requirement of high quality for aquatic recreation, and at the same time being destructive of that quality. (a) There is a need for a predictive model relating density of lake usage to lake water quality. (b) There remains a need for specific predictive models of the loss of septic field nutrients into the aquatic environment. (c) There is a need for a better understanding of the nature of water-based recreation. That is, what are the more important value judgments people make in their recreation, and where does quality of water enter into their thinking.

3. Energy demands in all forms continue to have a large impact on aquatic environmental quality. (a) Future demands for electrical energy may be met largely by nuclear reactors. Research needs include loss of radioactive materials into aquatic ecosystems, impact of waste heat, use of waste heat in fish culture, etc. (b) Despite this future shift, there remains a need for the impoundment and flooding studies currently underway. (c) Fossil fuel-fired generators carry the added problem of waste gases and trace metals entering the atmosphere and returning to ground and surface water. (d) A research plus monitoring effort will be required, for example, as tar sands petroleum plants come into operation with their large output of sulfur dioxide.

4. Agriculture has a great demand for water and is destructive of aquatic environmental quality. (a) The chemical fertilizers used in agriculture can have a great impact on water quality. There is a need for research into technology that would minimize the leaching of these nutrients. (b) Agriculture uses a great variety of chemicals as control agents and many enter the freshwater ecosystem. There remains a need for alternatives to some agents still in use. (c) Soil erosion via agriculture, especially potato culture, is great and research is needed into techniques to minimize this. (d) Feedlots on streams affect water quality adversely and mechanical destruction of the habitat by beef animals can be great. The impact of such feedlots needs to be monitored/researched. (e) Irrigation increases the amount of minerals in solution in ground and surface water. A better knowledge is needed of the extent to which this occurs and the effects on the freshwater ecosystem. (f) Wetland drainage continues in agricultural areas with little understanding of the total impact of this activity. Research is needed on the effect on waterfowl, aquafer regeneration, microclimatic changes, stream discharge, and many other aspects.

5. Forestry practices are still destructive of the aquatic environment. (a) There is a need to assess the impact of logging on stream production of salmonid fishing. (b) Little is known of the effect of logging on the leaching of nutrients from soils. (c) Logging dams are still in use in some parts of Canada, and the impact of these structures is poorly understood. (d) Forest insecticides proved very damaging to the aquatic ecosystems. The most destructive agents are no longer in use, but each new agent requires an extensive amount of research prior to acceptance. (e) Research in Canada has yielded a design for a completely closed pulp and paper plant — a plant with zero effluent water discharge. Research into this kind of technological innovation should continue to be encouraged. (f) Mercury has proved to be the most horrifying material used in the industry. Plant losses are now small, but research into the movement of mercury through the ecosystem must be continued. (g) Some fisheries are now closed due to high levels of mercury in the animal tissues. A research effort is warranted to determine if the muscle mercury concentration of tuna or swordfish could be reduced to an acceptable level during food processing.

6. The mining industry has a great variety of impacts on aquatic environmental quality, necessitating a diversity of research efforts. (a) Research must continue on the effects of mine waste waters, especially on aquatic organisms. (b) Mine tailings disposal in water is becoming less common and this research may be reduced soon. (c) Air-borne pollutants from smelters have had a great effect on aquatic ecosystems both in the form of acid precipitation and via heavy metal deposition. A continuing research effort is warranted, especially in view of the scope of the problem. (d) A major research effort into the technology of sulfur dioxide and heavy metal recovery is warranted by smelters that have not yet converted to pollution-free technology.

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The original Committee on Aquatic Environmental Quality consisted of Dr D. A. Chant (Chairman), Drs G. H. Geen and R. R. Logie. This group was succeeded by Dr L. Berlinguet (Chairman), Dr R. D. Connor and Mr B. McMillan. As the background studies approached completion, the Committee was expanded by five more persons, Mr I. K. Fox and Drs R. R. Logie, K. H. Mann, L. Rousseau, and J. B. Sprague. These people reviewed the draft of this publication in the preparation of their recommendations to the Fisheries Research Board as a whole. The comments of the eight people of the expanded Committee were incorporated in part or in total, into the final draft of this background study. The author is very grateful for the wealth of advice from the Committee.

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Appendix 1. National Research Council of Canada Grants-in-aid of Research Closely Related to Aquatic Environmental Quality

Effects of pollutants on the behavior of salmonids	$4,000
Water pollution control by fermentation of waste carbohydrates	6,580
The significance of bdelloribrio bacteriovorus in the ecology of polluted water	9,000
Aspects of environmental biology and pollution in relation to a changing environment in Long Pond, St. John's, Nfld.	2,500
Pollution in soil and water	5,000
Limnology of polluted and other running waters in southern Alberta	8,000
Environmental physiology of fishes. Effects of acidity on fish populations of La Cloche Mountain lakes. Factors influencing formation of circuli and annuli on fish scales	8,000
Environmental influence on fish ecology and behavior	12,000
1) The effect of light quality on photosynthesis and metabolism of freshwater plankton algae	
2) The effect of nutrients derived from agricultural drainage on eutrophication in Lake St. Clair	4,000
Water pollution abatement research	8,200
1) Removal of phosphate from wastewater	
2) Removal of sulphur oxides from stock	
3) Liquid	4,000
Limitations of systems for water pollution abatement	8,000
1) Destructive chemical oxidation in wastewater	
2) Gas holdup in water organic mixture	4,125
Evolution du mercure et de ses composés en milieu aquatique	4,000
1) Water quality changes through Mactaquac Dam	
2) Changes in dissolved gases through Mactaquac Dam	
3) Application of chemicals in the removal of solids from potato wastewater	7,000
A) The occurrence and distribution of metallic pollutants in air, soil, and water around Sudbury and Metropolitan Toronto	
B) Experimental study of uptake and distribution within plants of heavy metals including algae	
C) Interaction of moisture stress and nutritional disorders on transpiration	11,000
1) Bilan thermique d'un écoulement en nature	
2) Modification du régime thermique de la rivière Canaan et conséquences biologiques	5,000

Appendix 2. Other NRC Grants Relevant to Aquatic Environmental Quality

NEGOTIATED GRANTS

Research in coastal zone productivity environmental and genetic aspects	$119,000
Ottawa River project	101,000
Great Lakes Institute	75,500

REGIONAL DEVELOPMENT PROGRAM — SPECIAL GRANTS

Le recyclage des substances nutritives par per le traitement biologique sélectif des eaux usées dans le programme d'assainissement descaux du Saint Laurent	18,000

CONFERENCE GRANTS

International conference on transport of persistent chemical in aquatic ecosystems 1974	1,000

Aquatic Environmental Quality: Toxicology[1]

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[1]This report was prepared for the Fisheries Research Board of Canada. The views expressed are those of the author and not necessarily those of the Board.

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Abstract

HAMILTON, R. D. 1976. Aquatic environmental quality: toxicology. J. Fish. Res. Board Can. 33: 2671–2688.

Canadian research and control activities regarding the impact of toxic chemicals on aquatic environments are reviewed. Evaluation of specific research programs or results is not treated but an attempt is made to raise and discuss issues common to the problems posed by the use of toxic chemicals.

Résumé

HAMILTON, R. D. 1976. Aquatic environmental quality: toxicology. J. Fish. Res. Board Can. 33: 2671–2688.

L'auteur passe en revue les travaux de recherche et de contrôle concernant la répercussion des substances chimiques toxiques sur les milieux aquatiques. Il ne traite pas de l'évaluation de programmes de recherche ou de résultats spécifiques, mais soulève et analyse les points communs que pose l'utilisation des substances chimiques toxiques.

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Introduction

THE Fisheries Research Board of Canada's interest in matters relating to pollution dates back almost to its inception. Indeed, the Board honored the 50th anniversary of the National Research Council by issuing a special volume composed of selected papers back to 1902 that dealt with pollution (Fisheries Research Board of Canada 1966).

This interest has had an impact on pertinent world literature disproportionate to Canada's general scientific effort. In reviews (e.g. Pimental and Goodman 1973; NAS 1973) Canadian efforts are frequently cited as definitive. Usually these citations are confined to areas that, through time, have become recognized as key issues. For example, in the reviews above, all the aquatic animal behavior studies cited were by Canadian authors and almost all were published in the *Journal of the Fisheries Research Board of Canada*. Coupling this observation with other papers by Canadian authors that were not cited, one concludes that Canada has some claim to leadership in several fields relevant to pollution. Similarly, J. R. Brett's work, so frequently cited, was included as the definitive work on thermal effects in the recent effort to set criteria in the U.S. D. F. Alderdice's work has set world standards as well as that of M. Waldichuk. Although not original research, J. B. Sprague's reviews are recognized worldwide as key reviews in this particular problem area.

These comments should not inflate the ego of the nation, because the efforts of Sweden and its environmental agencies easily rival and frequently surpass our impact in these matters. They only illustrate the fact that Canada's long-standing concern and effort on pollution issues have had a large impact on the scientific community.

It is therefore appropriate that the Board, at this time, should commission a study to: review and assess Canadian research activities regarding toxic chemicals and complexes of such chemicals in the aquatic environment. Particular attention is to be focused on the division and coordination of responsibilities and activities among international agencies as well as domestic agencies such as universities, provincial and federal groups. Discuss mechanisms for assessing new chemicals that appear to have potential as contaminants and the adequacy of "early warning" systems which might prevent crises such as mercury.

The proposed objective is so broad as to preclude study and assessment of all suggested topics. Division and coordination of responsibility was largely beyond the scope of these studies because of time and the fact that no coherent division of responsibility appears to exist provincially, nationally, or internationally. Mechanisms for handling the challenges posed by use of toxic chemicals are chaotic, to say the least.

Consequently, the study concentrates on aspects of what I call "aquatic environmental toxicology" to the detriment of other fields such as analytical chemistry, monitoring, and transport. A focus is placed on the use of organisms as indicators or predictors of chemicals in the aquatic environment. To paraphrase Loomis (1974): environmental toxicology is, therefore, that branch of toxicology that deals with incidental exposure of biologic tissue to chemicals that are basically contaminants of the environment, food, or water. It is the study of the causes, conditions, effects, and safety limits of exposure to chemicals.

Even with this narrow view of the total prob-

lem the author was inevitably drawn from considerations of research to much broader issues. Therefore, this document does not attempt to treat, discuss, or evaluate specific projects or their results. It attempts to raise issues that are important to anyone approaching the problems posed by toxic chemicals in aquatic environments, irrespective of individual activity or discipline.

Scope and Scale of the Problem

In drafting this section one might be accused of dealing in scare tactics, such as found in unreasoned popular articles. This is not intended. A few facts are stated to add perspective to the issues.

You might recall pictures taken by the Apollo flights of the "spaceship Earth." These pictures of the blue and white planet against the black backdrop of space clearly demonstrate a system that is closed in every sense except energy exchange. Man's activities in this system have attained such a scale and intensity that he can now affect continents and even the globe itself. Moreover, one need not invoke the total world community; a single industrialized nation is capable of creating global problems. It has been estimated that Canada contributes over 5% of the SO_2 loading to the world atmosphere and most appears to originate with a single industry — base metal smelting (Summers and Whelpdale 1975).

Simply stated, there are two major problem areas: 1) use, disposal, and dispersion of specific chemicals, and 2) industrial and domestic effluents (aerial and aqueous) of mixed, variable, and changing chemical composition.

In the matter of specific chemicals it is possible to cite fairly precise figures. Approximately 1.8 million chemical compounds have been synthesized by man, about 9000 of these are produced in amounts exceeding 2000 pounds annually, and in excess of 10,000 compounds are in what is termed "commercial production" (more than 100 pounds per year) (Gillette 1974; Scott 1974). As relatively few of the 2 million chemicals have been tested for such an important aspect as carcinogenicity, one can reasonably suspect that environmental issues have been explored in very few, and only in the most obvious instances. Moreover, instances of detailed environmental assessment have been capricious. Why was nitrilotriacetate (NTA) tested to extinction when vinyl chloride (VC) was not, especially when one considers that production of VC is many times that projected for NTA? Why was TFM accepted as lampricide and dispersed into the Great Lakes Basins on a large scale without significant mammalian testing until many years following its initial use?

Suppose we perform a detailed assessment of all chemicals judged likely to affect the aquatic environment. Suppose we ignore all current production and use of synthetic chemical. That is to say, forget about the existing 10,000 chemicals produced in the U.S. alone (plus 1000 chemicals in 60,000 different formulations) (Kearny in Khan 1973); the 137 billion pounds of synthetic organics (120 billion pounds of vinyl chloride alone) produced in North America in 1970, a production increasing by 10% each year (Stoker and Seager in Khan 1973); the volatilization of gasoline and dry cleaning fluids to the atmosphere, as well as the province-wide use of forest pesticides in New Brunswick and the production of $8–10 \times 10^8$ pounds (1968) of phthalate esters (NAS 1973), compounds known to be persistent and toxic to aquatic organisms.

If it were acceptable to society that such products could be considered past history and, therefore, of little current interest (remember mercury), the fact remains that new chemicals are synthesized at the rate of 25,000 per year or about 500 per week. Of these, eight are seriously considered for production each week (Scott 1974). Between 1968 and 1974 about 2000 new chemicals were actually brought into production, so it can be assumed that roughly 75% of the compounds do reach production scale. In sum, about 300 new chemicals can be expected to reach production scale each year.

Assume further that only 10% of these compounds can reasonably be perceived as threats to the aquatic environment in any way, then it can be projected that Canadian government environmental agencies should, in some way, be concerned with about 30 novel chemicals annually. This is a judgment on one chemical every 12 days. This is appalling; a simple 10% error in judgment either for or against a compound could result in one severe economic consequence and/or ecological disaster per year. To render judgment on this scale is impossible, given present or even optimistic projections of future resources. Consequently, priorities are necessary, established on a set of scientific criteria.

The problem of industrial and domestic effluents is much more difficult to place in a meaningful perspective. If present trends continue, most fresh waters in the U.S. may soon be composed essentially of treated sewage. The toxicity of these wastes is variable, depending on the industry or industries in the particular water basin under consideration.

The problem is daunting, both in complexity and sheer scale of effect. Not content to pollute localized bodies of water we have graduated to larger scale efforts. Large marine areas are now little more than saline sewage treatment facilities. Other large areas are threatened with a similar fate (e.g. the Gulf of St. Lawrence). The present level of threat is also seriously affecting major areas such as the Baltic, North, and Mediterranean seas, as well as the Gulf of Mexico. In fact, we are quite capable of affecting the world ocean (SCEP 1970; Hood 1971).

Moreover, reasoned opinions have been presented concerning the ability of the atmosphere to translocate pollutants on a global scale (e.g. DDT, SO_2, HCB) and of our ability to modify the atmospheric envelope itself (e.g. fluorocarbons, carbon dioxide).

Man is now a geological agent, a description originally expressed by Dr E. Goldberg. Our activities are producing material loadings to our fresh waters, oceans, and atmosphere that markedly exceed natural processes. These ideas are appearing in science literature. A single example is the table cited by SCEP (1970). It treats a single specific issue, mining, and lists man-induced rates of material mobilization that exceed geological rates as estimated in annual river discharge to the oceans (thousands metric tons per year):

	Geological rates (rivers)	Man-induced rates (mining)
Iron	25,000	319,000
Nitrogen	8,500	9,800 (consumption)
Manganese	440	1,600
Copper	375	4,460
Zinc	300	358
Lead	180	2,330
Phosphorus	180	6,500 (consumption)
Molybdenum	13	57
Silver	5	7
Mercury	3	7
Tin	1.5	166
Antimony	1.3	40

As pressing as these concerns are to man, what are the effects on fish? Specifically, they are the stocking of the Great Lakes only to produce PCB-laden fish, the high productivity of Lake Erie which results in the increased production of coarse fish or fish unacceptable to sophisticated markets, and the acidification of lakes with the resultant loss of sport and subsistance fisheries.

The Canadian marine fishery is a productive industry and an important protein source. It has also been called a carefully disguised welfare scheme. In either event, it must be preserved, and in this context SCEP (1970) can be cited:

> "The present threat to marine fisheries lies not so much in the danger of polluting the grounds where the fish are caught but in the pollution of inshore areas where many species reproduce. These nurseries are being dredged, filled and polluted with nutrients and heavy metals. The value for commercial yields becomes a cost to be considered in evaluating policy for estuaries and coastal oceans."

The issue of contaminants and their impact on fisheries poses large and complex problems. There is little evidence that these general problems are being tackled in any coherent, logical manner at present, although excellent work is being done on specific problems and problem areas. Moreover, there is little evidence that the consequences of introducing new chemicals, or adopting policies toward effluent discharge, are being considered in decision making in a comprehensive meaningful way. This is not to say that certain site-specific issues are not resolved adequately but that the overall policy and problem evaluation appears deficient.

The actual utility of past efforts to resolve specific issues must be adequately documented for management. It would seem appropriate that the services of the Department of the Environment (DOE) begin a systematic effort to relate the use of toxic chemicals and the discharge of effluents to changes in the productivity of ecosystems under their mandate. Perhaps this effort could begin by focusing on the relationship, if any, between the implementation of the effluent regulation program and specific improvements in the quality of Canadian aquatic environments.

Responsibility and Coordination

Most Canadian research on aquatic contaminants is by the federal government.

Within government, the Department of the Environment is the major agency, mainly through the activities of Fisheries and Marine Service, Canadian Wildlife Service, and the Inland Waters Directorate. A précis of the roles of these groups is in the Canada Water Yearbook (1975). However, through contracts or grants the Environmental Protection Service (EPS) of DOE, the National Research Council (NRC), and the Department of Indian and Northern Affairs (DINA) also support research. The Ministry of Transport is charged with the prevention and cleanup of oil and other pollutant spills in marine areas, but there appears to be little research activity except

in the matter of technology development. The National Harbours Board may be similarly described.

Since the government reorganization in the 1970s, the Minister of the Environment has been responsible for approximately 80 different Acts, portions of Acts, or regulations under Acts. Of the 80 pieces of legislation, about 15 have to do in one way or another with environmental contaminants. Ten are directly concerned with contaminants as they affect aquatic resources rather than contaminants as they affect man.

In practice it is difficult for the uninitiated to determine which Minister actually controls certain Acts. This issue is especially difficult with the Department of the Environment and the Department of Indian and Northern Affairs in their legislative roles "north of 60." Although a major issue to people involved in enforcement, it has been a minor irritant to research people to date. However, it may soon become a major impediment to research in the arctic. More research effort is needed in the arctic and funding must be freed from jurisdictional battles; it must concentrate on key issues, not on who is employed by whom.

In any event, many pieces of legislation relate to the DOE effluent regulation program of the Environmental Protection Service (Anon 1974). Under this program regulations are promulgated in consultation with other federal and provincial agencies and industry. Research in aquatic toxicology enters the process mainly through the development of fish bioassays for various industries, and through setting toxicity limits for appropriate regulations.

These regulations bear no relation to the quantity or quality of the waters receiving the effluent. They are based on "best practicable technology," an engineering term that has little direct significance to environmental issues. Although designed to reduce discharges and to prevent the occurrence of "pollution havens," their main effect appears to be the tentative chemical or biological standardization of effluents across the whole of Canada. Reduction of discharges or the toxicity of discharges is laudable but the idea that these regulations are significantly protecting the environment has not been generally substantiated to my knowledge.

Some provinces also have legal regulations for industrial effluents, sometimes more stringent regulations than those of the federal government. Moreover, some provinces have other legislation concerning protection of the environment. Traditionally, scientists have not been concerned with legal matters, but research people are tackling current problems. This tangle of legal instruments does have bearing on their work and a précis of pertinent legislation as well as appropriate explanations would be appreciated. As usual, Sweden has set a precedent (Lundkvist 1974). However, a very brief Canadian exposition is available of federal, international, and provincial agencies as well as pertinent legislation (Canada Water Yearbook 1975). Although well intended and sufficient for the audience of the Yearbook, it is unsatisfactory for the audience that I suggest be addressed.

Recently, an Environmental Contaminants Act was passed by parliament. This act is similar to one passed by Sweden in 1973 and if enforced (the ministers have authority on some matters but are not required to act), it would markedly enhance the ability to control the distribution, use, and disposal of toxic chemicals. An excellent précis of the background and history of the development of the act has been prepared by Dr J. C. Macleod of Fisheries and Marine Service but, to my knowledge, it has not been published.

In past years, Canadian governments have been faced by environmental crisis after environmental crisis and they usually responded as quickly and as thoroughly as circumstances and the ministers directed. However, the results of this ad hoc response are the proliferation of many environmental programs that are either reoriented residues of old crisis programs or are attempts on the part of national or regional management to anticipate issues.

Some existing research programs overlap, but it is difficult to define either the degree of overlap or the frequency with which it occurs. No special reason exists to consider overlap necessarily wrong. In fact, it may be laudable under certain circumstances. However, there is a lack of formal communication between these projects except in the sense of publications and "underground" networks, and governments would be better served if formal communications existed. Nevertheless, some efforts at coordination exist, which are not specifically related to research. A good example is the Federal Interdepartmental Committee on Pesticides that functions effectively. Various other committees exist; for example, those concerned with the use of forest pesticides, biting fly control, and mercury in the environment. Government's response to many issues is to form a committee. The efficacy of these committees to coordinate research is suspect for they seldom possess management capability. An exception to this is the Alberta oil sands environmental research program's steering and technical committees. This organization is a good example

of strong coordination to attempt a resolution of an environmental problem involving contaminants. Federal, provincial, university, and public research work will have to be welded by these agencies into a single program. Its degree of success remains to be seen and is largely dependent on the key individuals involved.

Canada is involved with international organizations and agencies, particularly in the marine field (e.g. Waldichuk 1973), but some involvement also exists regarding fresh water (Canada Water Yearbook 1975). Any coordination, however, is due to the goodwill of the parties concerned as few binding agreements appear to exist.

There is little evidence of comprehensive national liaison in these matters, although some liaison does occur within the higher management levels of federal and provincial governments. The productive functional level is probably that of the research scientists, and management coordination on functional basis is quite rare.

The situation is generally healthy. However, some improvement could occur in coordination if there was a way to establish governmental priorities in contaminants research. These priorities could be discussed and a consensus reached which could be communicated to the appropriate research components, both internal and external to government. This aspect is discussed elsewhere in this perspective.

Finally, in Canada there are a number of groups concerned with the practical and legal aspects of environmental contaminants. Unfortunately, in Canada there is also a tangle of federal, provincial, and municipal legislation regarding pollutants in the aquatic environment, but there is no description of federal and provincial agencies with their precise assigned roles. It would seem appropriate for Canada to imitate Sweden by publishing clear, concise, and nonlegal descriptions of existing legislation and the responsibilities of key agencies, for consumption by the lay public and by concerned scientists. Such efforts should be delegated to a university or other legal communities external to the federal government. It would also appear that both DOE and DINA have been delinquent in defining their roles in the arctic in a manner conducive to the most efficient resolution of problems.

Level of Canadian Effort

New problems inevitably produce requests for new resources; thus, one of my first concerns was to try to establish the extent of Canada's present investment in manpower and dollars. This proved to be remarkably difficult in spite of the simple nature of the question.

1. The investigation of environmental contaminants and aquatic toxicology involves a wide variety of fields and disciplines. Activities are described by their proponents in very different ways. Moreover, the activities are distinct in certain ways and overlap in others. Thus, definition is a real problem.

2. The main investment is by the Government of Canada. This institution is remarkably cavalier in relating expenditures to well-defined activities. Data concerning sets of activities (e.g. "goals" or "objectives") are available, but their definition is so broad they are almost useless for this exercise. In addition, program descriptions may change with changing goals, program activities may not.

3. A number of surveys available (FAO 1974) depend on the interest, comprehension, and veracity of those questioned.

Surveys seem to be a serious preoccupation of international agencies and are suspect as a substitute for real research. In any event, these surveys and those conducted by government of its own activities suffer from a pronounced lack of attention to analysis of the basic data and editorial detail. As currently conducted, they fall well short of perfection and may even fall well short of utility.

Having delivered this apologia and confessed to some frustration, what follows constitutes the selected information compiled within the time available.

This country has turned large portions of its research activity to pollution problems in the last decade. The shift is very pronounced in government laboratories, but is hard to detect in the academic community, as these changes usually constitute minor conceptual shifts in individual research activity.

Although quantification is difficult, some data can be cited. In 1970–71, NRC conducted an inventory of pollution-relevant research in Canada (Sutton et al. 1972). The authors made no claim to completeness, but obviously they made every attempt to cover as many areas as possible. This document was searched, using a selected set of key words that, in my estimation, provided maximal output. This output was then analyzed and workers who focused on aquatic toxicology were selected. Of those responding to this survey, about 100 people could be considered actively engaged in research in this area. Most were employed by governments (60), with the federal fisheries component (mainly what was then the Fisheries Research Board of Canada) contributing 30. The remainder were largely associated with universities or with consulting firms.

Regrettably, no more recent inventory was available to the author. However, in 1974 about

50 people attended a Freshwater Institute Symposium on aquatic bioassays. The 1975 version of this symposium, held in Ontario, attracted even more (Craig personal communication). In 1973 about 100 people met to consider oil and the Canadian environment — of course not all were aquatic scientists or scientists interested in toxicology (Mackay and Harrison 1973). In 1974, some 100 Canadian researchers gathered to consider the transport of persistent chemicals in aquatic ecosystems (de Freitas et al. 1974). An FAO survey (FAO 1974) recorded about 21 Canadian institutions engaged in investigations regarding contaminants in aquatic organisms. Not all have bioassay expertise and many are concerned about contaminants affecting fish as food. Time did not permit an evaluation of provincial personnel or those in consulting agencies, although both areas are represented in the documents cited above.

To proceed from these considerations to expenditures — it is a matter of record that contracts are let by the Department of Supply and Services for other departments. The published record of the contracts was reviewed for the nearest annual period to this study. It is difficult to ascertain from a title and an abbreviated description the exact purpose of the contract, but approximately $1.7 million were expended on matters pertaining to the environmental impact of toxic chemicals, chiefly oil.

The contracts varied in price from a maximum of $470,000 to a minimum of $500. One would suspect from the titles of the two contracts that the cost should be reversed but, most contract costs seemed quite reasonable for the problem described, the average cost being about $22,000.

As could be expected, the Department of the Environment was by far the major contractor, and let some $1,360,000 in contracts. Surprisingly, the Department of Indian and Northern Affairs was second with $300,000, and other Departments fell far behind. These figures are based on the census of a single year and trends in government spending established in this manner are difficult to project.

Curiously, in completing this survey with an additional spot check on 2 more years of statistics it was not possible to find one instance of the Department of Regional and Economic Expansion letting a contract reflecting any environmental concern. Considering that this Department is a large-scale promoter of industrial expansion, one wondered what mechanisms are used to establish the impact of its many and varied projects. Apparently, such studies are conducted by the proponent and, thus, appear as studies by other agencies or private concerns. Data on this latter category were unavailable because of the proprietary nature perceived by most companies. Provincial expenditures were also largely unattainable in time available.

The following estimates were made of other federal expenditures:

The most recent NRC Directory of Federally Supported Research in Universities was reviewed using selected key words. It is estimated that some $600,000 are being expended annually via this route, with contracts and grants ranging from $1000 to $103,000.

Estimations of federal in-house expenditures are always debatable. For example, a recent survey of resources expended by Fisheries and Marine Service (FMS) on environmental problems (excluding contaminants in fish as food but including a major component dealing with oil), led to the estimate that approximately $2,000,000 and 100 man-years were applied to this area annually. This estimate was challenged for being too high, yet it was based on a rigorous and restrictive analysis of the Service project records. Admittedly, the survey was predicated on the assumption that the project codes used were reasonably precise, and that all project leaders used the correct code and not the code they deemed to be popular with management. It has been suggested that neither assumption is safe but it can be argued that this estimate cannot be far wrong and may even err conservatively.

The FMS 1974–75 budget exercises were also reviewed regarding certain selected goals and targets. Some personal judgment was used to estimate there is an expenditure of about 175 man-years and $3,500,000. It must be stressed that this estimate extends to areas well beyond aquatic toxicology but does appear to include most activities related to contaminants as they affect the resource, not as they affect fish as food. It may also include nonresearch activities.

To employ a crude estimate on the whole of DOE, of the approximately 650 research scientists employed, about 300 are in services directly concerned with the aquatic sector (Inland Waters, Fisheries and Marine Service, and surprisingly, the Environmental Protection Service which has no research mandate). Extrapolating from fairly firm knowledge of certain establishments I would suspect that 15% of DOE scientists are directly or indirectly involved in the study of toxic chemicals. This estimate might include some scientists concerned with pursuing research problems related to toxicants as they directly affect man.

Assume a figure of 100 research scientists in DOE is correct, and that $50,000 is a fair estimate of the cost per scientist, one can estimate

that the department, as a whole, may spend upwards of $5,000,000.

This total seems low compared to the figure derived from FMS alone but it should be stressed that it refers solely to research. If one goes through a similar exercise based on the FMS complement of about 210 research scientists, one can derive an estimate of 30 research scientists and an expenditure of $1,500,000 annually.

No access was available to expenditures on similar matters in the Canadian private sector. While much testing of toxicants is done in other countries at the present time, our environmental impact review process requires that some consideration be given to the use of such chemicals. Private expenditures on research are probably considerable and climbing, although this proposition depends heavily on how one defines research.

The net picture gained from these estimates is of a fairly large and active scientifically community within government and within the country. Moreover, data suggest the expenditure of considerable sums of money on pollution-related problems and on pollutants as they affect the biota. However, it is stressed again that the data are diffuse and so Canadian investment in this sector remains unclear. This state of affairs constitutes less than optimal management of research resources and poor management of what is a crisis issue.

It is essential that the Federal Government make a concerted effort to identify the level of human and other resources devoted to the question of research on, and control of, contaminants in the aquatic environment. Without such data there is no realistic way of reaching a reasoned management decision regarding the reallocation of research resources to resolve specific problems. Moreover, without such data and a reasoned list of priority issues, it would be unrealistic for management to approach the citizen for increased research or management resources.

The Proponent Pays?

Implicit in many pieces of legislation and in the attitudes of many governments (e.g. Canada, U.S., Sweden, and Great Britain, at least) is the concept that the polluter or the proponent pays. On the surface this seems an eminently sensible attitude. However, there are issues at stake which deserve intensive, albeit chiefly economic research, as well as a reevaluation of decisions at the highest of management levels.

The problem is that while the public is demanding the benefits from new industrial developments and from the use of new chemicals, it is also demanding better protection of the environment from the hazards posed by such developments or chemicals. Government response to this legitimate desire for enhanced protection is to implement stricter controls, environmental impact assessments, and the requirement for ever more thorough testing of chemicals. All these impose a burden on the proponent, a burden that is becoming very large indeed. To quote from Djerassi et al. (1974):

> "Despite the recent publication of many papers concerning the high cost of developing new pesticides, figures are hard to generate for individual products because of the proprietary nature of such information. In 1970, a survey of the pesticide industry claimed an average cost of $5.5 million for the development of a new pesticide. The time required for commercialization was 77 months. A similar survey of 14 companies reported an average cost of $44 million in 60 months in 1969. As pointed out correctly by Johnson and Blair, these figures are too low since they do not include the cost of pilot plants, process development or studies of waste control and other environmental factors. Their more realistic estimate leads to a figured $11 million over ten years which includes not only the cost of developing unsuccessful compounds, which must be borne by the successful ones, but also the additional costs involved in the failure to invest $11 million at 8% if the company had instead chosen merely to deposit the money in the bank."

This estimate is close to the $12 million quoted by the soap and detergent industry for the development of nitrilotriacetic acid (NTA) as a phosphate replacement. Moreover, environmental research work related to the oil sands development in Alberta has been estimated at $30–40 million over a 10-year period.

Although not all the costs regarding the development of a new chemical can be charged to proving environmental safety, it is certain that a large fraction of the investment goes toward dealing with such concerns and this cost is increasing.

Perhaps industry should accept these costs but it is doubtful if policy makers are aware the burden acts as an economic selection process which may not be in the best interests of the country.

In discussing these issues, it is necessary to separate the concept of responsibility from the argument. The proponent is certainly responsible for proving the environmental safety of the product and government is equally responsible for dictating to the proponent how to present such proof

and what degree of risk is acceptable. Costs of these activities are the issue for the business enterprise and the alternatives require decisions by government. Such decisions would require preliminary investment by government in socio-economic research to provide a good data base. It is doubtful that such research is currently underway in Canada.

One consequence of high costs is that only the large companies can afford to remain in business. Only they can afford the huge outlays and to tie up such massive blocks of funds for long periods of time. Thus, a selection process is imposed on the industry itself and it seems reasonable to suggest that this deserves some debate, especially in view of the thought that we may be actively selecting against Canadian industry.

Once the large companies have been selected another effect emerges — the larger the company, the larger the market must be for a product to be attractive. Djerassi et al. (1974) cited one example where this effect emerged and work on a promising pesticide was discontinued. In this instance the company even offered to donate the patents and rights to the state but the state could not accept.

An additional selection process is exerted by cost on the types of chemicals produced. For example, narrow spectrum pesticides are not developed unless the pest species is widespread or attacks a crop of major economic importance.

Moreover, it is cheaper to prove the environmental safety of a wide spectrum, low toxicity pesticide, than a narrow spectrum compound with, perhaps, relatively high toxicity. In spite of the desire to avoid the former with their impact on nontarget species, we may be economically encouraging their continued development and production.

Another consequence is that an agriculture such as ours, addicted to pesticides (e.g. Whelan 1975), continually requires new ones and these are not being developed. This fact has penetrated government to the extent that concern was recently expressed regarding the lack of new soil pesticides (FICP 1975), and the observation was recorded that "environmental considerations and regulations had dampened the enthusiasm of the manufacturing companies for development work due to the uncertainty of realizing an economic return," an observation not agreed to by all participants. However, the net result of such basically economic decisions is the continued manufacture and use of compounds known to be environmental hazards.

The view has been expressed that universities and government could generate data for pesticide registrations. The concept, if applied to government laboratories, appears to be contrary to present policy within certain services but is actively embraced by other services and departments. It is unlikely that most university people would be interested because the short-term dollars would not assist training graduate students. There is some sympathy in government circles for the position of the companies which is by no means restricted to this particular case. However, there seems to be little if any attempt to develop concerted action to resolve the problem.

Fischer (1974), in his review of an analogous issue (the environmental impact assessment process), made the point that such costs are a minor problem compared to reaching a suboptimal decision (optimal defined as the reduction of adverse environmental impacts). He further suggests that direct costs of assessments would decrease with increased experience as would such indirect costs as those associated with the delay of a project. The analogy becomes somewhat strained at this point because it would appear that increased experience in the field of toxicology has resulted historically in a demand for more assays as well as assays of increased sophistication; both demands result in higher costs. Fischer's main point is that the assessment process itself acts as a control process. Similar sensitivities have been expressed by the Canadian fishing industry during a recent symposium (Nelson 1973) and it has been suggested that emotion, not common sense, is a determinant (Fahnestock 1969).

Government indecision in these matters is becoming a subject for some debate in the scientific literature (e.g. Anon 1975). If it is being debated in these circles, one can be absolutely certain that it has been debated for some time by the industries concerned.

Therefore, it can be suggested that the side effects of environment protection are becoming major selective forces within the affected industries and have become a serious factor in industrial decision making. It is proposed that it is time for governments to review their policy in these areas because strict adherence to the "polluter or proponent pays" may not be in the public's best interest. This is proposed because there is little or no evidence of formal effort to consider the concerns outlined above or to explore the increasingly obvious reluctance of industry to engage in new research and development activities regarding control agents. To quote Djerassi et al. (1974): "Policy makers then ought to consider whether special incentives are needed to stimulate the conduct of practical work in these areas or whether other sectors of the R&D com-

munity could contribute effectively to practical new approaches in these fields. *We make the categoric prediction that, if this is not done properly, most current public pronouncements on the likelihood of fundamentally novel human or insect population control agents will represent grossly optimistic exaggerations.*" (Italics mine.)

Various alternatives have been suggested in the U.S. and elsewhere to resolve these issues. This is not the proper forum for consideration of alternatives, but it must be recognized that costs associated with evaluating potential impact of industrial production of new chemicals are affecting the composition of the industries, their research activities, and decisions. Moreover, it is suggested that these costs may actually act as a selection process against Canadian industries in favor of large multinational corporations. Therefore, it would seem that the "polluter or proponent pays" philosophy is in need of debate and review to determine if strict adherence is still in Canada's best interest. Socioeconomics is probably the key research issue in this problem area.

Priority Setting

From the data presented on the rate of production of new chemicals, the costs of testing, and present investment in research, it is clear that Canada cannot afford to deal with all environmental contaminants problems in the same manner, nor carry them to the same degree of resolution. It is equally clear that industry cannot be loaded with an impossible burden, for to do so may actually mitigate against the best national interests. Moreover, it must be remembered that compounds required by government must be assessed by government, assays required by government must be developed by government, results from assays required by government must be checked by government. Almost all these activities could be called research or stated to be in need of research at the present time.

Consequently, within the research community and within the larger context of management of toxic chemicals, what is needed is a priority-setting mechanism that will generate priorized lists of toxicants for action by concerned agencies. Presumably, these agencies should then feed data to a final decision-making authority who balances need against the perceived level of risk.

The question is, how does Canada set those priorities?

The proposed U.S. Toxic Substances Act, the Canadian Act, and the Swedish Act all contain clauses that require industry to notify government of intent to produce or import chemicals. Government then is to decide which compounds require further data and can demand it. What is not currently clear is the basis on which government still decides that it has an interest. How is it to decide what are problems and what are nonproblems?

The Canadian government is attempting some action in this area and some action is apparent in connection with the Canadian/U.S. Agreement on Water Quality (Macleod personal communication). This is a key issue. It is suggested that priorities must be in place, at least provisionally, before any other action is taken under the Environmental Contaminants Act. Certainly, priorities must be set before requests for resources are made, for without a knowledge of priorities fiscal estimates of consequence cannot be placed before Parliament.

The literature contains a number of attempts to set priorities or to at least flag problems that concern informed individuals. Most of the better attempts appear to depend first on the desired level of protection required (NAS 1975) which, while basically a socioeconomic issue, is an important aspect of the decision-making process. Some assessment of potential risk must then be made (NAS 1975) in which it is recognized that no battery of tests or compilation of information can prove the complete safety of a chemical. It is suggested that, at this point, some estimate of benefit be considered, perhaps analogous to the human toxicologists use of effective dose (ED) in comparison with lethal concentration (LC). However, there is little evidence that this is done or proposed to be done even in such obvious applications as pesticides where an ED_{50} could easily be contrasted with, for example, LC_X data for man (LC_1, is probably untenable).

Both risk and benefit assessments will depend on such information as the relation between chemical structure and biological activity (Khan 1973; Veith and Konasewich 1975). Much use is made of the toxicity unit concept, developed by Sprague in his critical reviews of aquatic bioassay methodology (e.g. NAS 1973; Seba 1975). The relative acute toxicity concept (Loomis 1974) is finding some application as well.

Other attempts to set priorities, while recognizing toxicology data, deal with existing problems on the basis of scale and manner of use (SCEP 1970; Dryssen and Jagner 1972). This approach is particularly true of the oceanographic community. A recent Organization for Economic Cooperation and Development (OECD) effort used chemical class, source, and function to categorize but not to priorize specific chemicals recognized as water pollutants. Categorization, while

useful, is a pitfall to be avoided if priorization is really required.

This study does not recommend definitive criteria to be used in setting priorities. It is important that Canada develop its own priority setting mechanisms and priorities. The efforts of other nations should be appreciated and not duplicated. However, Canadian concerns may prove unique or, at least, different. Indeed, concerns arise peculiar to individual provinces or regions. Moreover, in Canada the risks are assigned to one department (e.g. DOE) while the benefits are assigned to others (National Health and Welfare, CDA); an invidious situation.

In the more restricted context of aquatic toxicological research there is no evidence of a comprehensive effort to set priorities for Canada. Research seems to be initiated on specific toxicants for three main reasons: 1) it is the current fad, 2) it is imposed by external authority because of its crisis nature, and 3) the individual scientist is perceptive enough to anticipate upcoming issues and is persuasive enough to sell a program to, or hide it from, management. This situation could be improved if there existed a list of toxicants which the Canadian government believed to be problem chemicals. Concerned agencies could then be guided by, but of course not restricted to, this list when funding in-house or external research activities.

The present use of chemicals, the rate of production of new chemicals, and the costs of testing indicate priority setting mechanisms must be developed as all chemicals cannot be assessed to the same degree. It is essential that decisions to test are not taken capriciously. As the assessment of potential environmental impact of toxicants will require research and research resources which are limited, the issue of priority setting assumes particular importance.

Information

Before initiating a research program a good scientist reviews the literature to establish what is already known of the topic. The recent information explosion has made this task difficult. In the field of pollution, the problem is compounded by the vast amount of data which is proprietary, restricted to government files, or contained in government reports. In 1974, the American Fisheries Society conducted a survey which suggested that 30–60% of research efforts on pollution abatement conducted by U.S. Federal, State, and Canadian agencies were never formally published. That survey also estimated that 8–16 months elapsed before information publication and 18–28 months elapsed before formal publication in a scientific journal.

Many current reviews are of little use to the scientist because they tend to be superficial and user oriented. Some, which take the form of a list of slightly expanded titles (e.g. McKinnon et al., 1974), contribute to the information explosion rather than ease a researcher's task.

In considering reviewed or unreviewed publications it appears that experiments today are increasingly constructed on data that are currently available to the researcher and not on all available data. No one wants to reinvent the wheel but redundant research is becoming increasingly common. When the cost of decisions to use or prohibit the use of toxic chemicals and the investment in research is considered, the issue of readily available information assumes major proportions.

A study was commissioned recently in Fisheries and Marine Service to "increase the effectiveness and efficiency of scientific and technical information and data service in FMS." Nowhere in the objectives, terms of reference, or memoranda accompanying the announcement of this study was any mention made of toxic chemicals and their impact on the environment. The author of this review approached one member of the study to suggest that this was a key area of interest to the service, to the Department, and perhaps even to the country at large.

Problems in human health have been addressed recently by a United Nations study group on health hazards from new environment pollutants. The interim report suggests that the major problem facing the scientific community is to bring scientific and technical information from the published literature and other miscellaneous sources to those who need it (in real time). They note an estimate of at least 3000 articles in the area of pesticides alone published annually; these appear in perhaps 250 periodicals. The report of this study group examines various toxicological information handling systems, but most seem applicable only to human toxicology problems. However, the report does flag the issue of industrial data which may be released only on assurances that confidentiality will be preserved. In summation, the report proposed that an international register of toxic chemicals be created. Canada participated in the discussions of this proposal, but national commitment depends on the level of expenditures that would be required from a developed country, in spite of the goodwill that this might generate among the underdeveloped nations. Because human health was the chief concern of this program, it did not appear

appropriate for environmental agencies to be involved. It is expected that the man-year resources required will be judged excessive by management because of this.

The problem of data acquisition is of such a scale now that it is doubtful if any one country can afford to acquire, sort, and disseminate all existing information. Moreover, there are some serious scientific questions regarding the types of data to collect and their relative merits. The problem is complicated by the fact that any data acquisition and dissemination system proposed for Canada should be compatible with the main international data handling systems.

Many public and private computerized information retrieval and data bases exist that deal with potential pollutants or toxicants. Unfortunately, most are concerned mainly with questions of human health. Consequently, the existing data bases are of little immediate use to the environmentalist and literature retrievals for environment tests must be accomplished by existing, general search systems. Even these systems may not enable one to search back more than a few years.

We seem to have proceeded beyond an information explosion to an information crisis and this is leading to duplicated research efforts. In view of the paucity of research resources in Canada and elsewhere, this seems to be weak management.

While access to the literature is a key issue to scientists, other data are also needed to set priorities to allocate research resources and to design experiments. This sort of data is not the consequence of prior research but of production and use, for example: molecular formula and systematic name, trade names, chemical characteristics; major formulations and their components; production methods including efficiency, chemicals used in the process, and, if at all possible, chemicals produced as by-products which are discharged in effluents; degree of purity of the product, contaminants, if any; uses proposed, scale of production and use, geographical areas of use, test sites used; major routes to the environment, disposal routes and methods; if a biocide, target species; mode of action, if known; chemical assays for the active agent and contaminants that are useful in the receiving environments and biota; bioassay data known to the manufacturer; persistence and transformation data known to the manufacturer; transformation products, chemical assays for such products if they too are suspect; data as above on carrier compounds or solvents.

Many of these data are considered proprietary by the companies concerned and if given to government, are unavailable to the environmental expert, even if employed by government. Access is an important issue.

Scientists have restricted access to production rate data because of restrictions such as those which govern Statistics Canada (FICP 1975). The proposed Environmental Contaminants Act may help as it does have an information clause (as does the Swedish Act). Even in the U.S. basic data seems less than readily available if one accepts as evidence the lack of production figures in NAS (1973, table IV-7). This lack of basic information was scathingly described during the recent Public Hearings into the Use of Pesticides and Herbicides in Alberta (Alberta Environment Conservation Authority 1974). The hearing found that government agencies that have data cannot share them with environmental agencies. Hearings in British Columbia have also expressed concern as has the U.S. National Academy of Sciences (NAS 1975) and other agencies (SCEP 1970).

The list of necessary data is basic and contains little reference to the environmental impact of chemicals, but many companies invest large sums of money in such studies. These studies and their data are often withheld from agencies such as DOE. These studies are done in good faith and with concern for the environment, but companies are afraid that the data will become available to enforcement agencies and be used against them in some indiscriminate manner. As someone said, they do not want to see a scientist open his lab coat to reveal a badge. While one can have some sympathy for their position, the conflict must be resolved. At present, DOE and provincial agencies expend large sums of money repeating studies already done by competent professional consultants to industry. This makes little sense as costs of both studies are eventually borne by the public.

It is suggested, in view of the current crisis in the management of scientific information regarding pollution and its consequences, that the Department of Environment explore the possibility of creating a data bank and information retrieval system, compatible with existing and proposed international systems. However, initially the department should explore the possibility of giving scientists increased access to existing systems. Care should be exercised not to expend resources on a "Canadian" system per se, and it may be that any system might be judged less than useful at present.

It is also suggested that Canadian scientists need access to data now considered as proprietary by industry, and that some real effort be made to overcome resistance to release of such information. This could be on a "need to know" confidential basis. Some real effort must be made to enhance information exchange on a confidential basis if necessary. Enforcement agencies may have to be excluded initially from such exchanges.

Early Warning Systems

Fail-safe early warning systems are a treasured myth of the public and the public servant who must face the wrath of the public when a problem explodes. There seems to be no instance in the world of a functioning system and one suspects we must consider not a single system but a composite of inputs to government. What may be needed is a central focus that, not being preoccupied with fire fighting or advising the minister and his senior officials, is free to contemplate the various inputs, flag issues, and especially marshal the minimal preliminary resources needed to define (not solve) the problem or nonproblem. (One scientist suggested that all that is really needed is to establish a senior scientist in Japan on the theory that such an individual would be personally involved in at least one-half the issues Canada will have to face.)

This issue was also addressed by J. E. Brydon of EPS before the Standing Committee on Fisheries and Forestry of parliament during its consideration of the Environmental Contaminants Act.

He stressed that some inputs to such a system are techniques, some are generalized approaches to problem solving, and others are categories of information. Various degrees of refinement currently exist among these elements. The following is much paraphrased from that of Brydon:

1. Intuitive judgement: based on research, speculative analyses, monitoring, and knowledge of chemical behavior in the environment.

2. Epidemiology: health effects observed in workers as well as plants and animals of economic use.

3. Episodes: catastrophic events such as PCB poisoning, or long-term events such as mercury pollution.

4. Screening systems: the simplistic information which should be available from industry.

5. Testing by industry: the mandatory, probably unsophisticated, assays which may be required by government.

6. Materials balances in industries: data on raw materials, efficiency of process, wastes produced, purity of product, unaccountable losses of material, etc.

7. Notification or mandatory reporting by industry of intent to manufacture, import, or use new chemicals.

8. International reporting: specific chemical problems in other countries; bulk oceanic transport of toxicants.

9. Specifically constructed lists of hazardous substances: key issues raised by the coordinated efforts of the science community.

10. Backward and forward tracking: colloquialisms that refer to the analysis of past events to relate cause to effect and to the attainment of a predictive capability.

11. Structure–activity relationships: a less than perfect method for predicting biological activity but one that is beginning to be useful.

12. Technological and econometric forecasting: prediction of changes in industry.

13. Modeling: use of mathematical models, ideally used to predict effects but usually used in backward tracking or physical models such as the Experimental Lakes program.

14. Biogeographical prospecting: the natural occurrence of metals in the biota or their environments, mainly used in North America to define problems not due to man. In Russia it is used to locate valuable mineral deposits.

15. Protocols: another word for Early Warning Systems? Usually confined to the assessment of chemicals prior to use. It implies the use of a wide spectrum of bioassays with some of the items 1–14.

Items 1 and 15 seem to be the inputs which can and do affect the decisions by governments at the present time. Intuitive judgment is really an integration of items on the list that are available to the individuals. Thus, individual scientists constitute early warning systems and the issue may be to ensure that they have better access to data suggested above.

Even when early warning data are available to governments it is frustrating that usually the media provokes action and triggers key decisions. Why then would one expect a comprehensive, formal early warning system to be useful? A broad ranging system to manage chemicals of ecological consequence may be essayed, but such a system should never be expected to anticipate all issues or exercise the intuitive leaps that constitute the chief utility of research people.

Consequently, formal early warning systems are probably fond but unattainable dreams at

present. It is strongly suggested that information is the key issue and, for the moment, we concentrate on perfecting the information needs suggested under points 1–15 and rely on informed individuals for the early warnings.

Some Specific Issues

Many groups have met to consider priorities for toxicants, issues, and chemicals. This study does not suggest an inclusive list of problem chemicals but raises some issues that occur repeatedly in literature and that should be of concern to Canadians.

In the matter of specific chemicals, comprehensive lists occur in NAS (1973) and certain key issues have been raised elsewhere (e.g. SCEP 1970). The recurrent topics have become familiar to most Canadians: mercury and other heavy metals, oil, PCBs and other chlorinated hydrocarbons, nutrient loadings to the oceans or fresh waters, nuclear wastes, and sulphur transport (chiefly the acid rain issue). To pursue specifics related to these broad topics would be repetitive here; however, they might be usefully considered by a priority setting group.

There are many other issues worthy of some Canadian research. Work may already be underway in certain areas and the suggested topics are not meant to include or judge such work.

Increasing amounts of metal contaminants introduced to the world's oceans are of concern to the marine science community. A great deal of this contamination is due to direct use of metals such as mercury, where half the world's total production is added to the ocean environment each year. Much is harder to quantify and track as it is caused by mining operations and related activities or the use of fossil fuels (e.g. Marine. Poll. Bull., 1975. 6(6): 81–96).

The impact of toxicants on aquatic predators is a concern not in the matter of reduction in numbers or in complete loss of species per se, but because of the probability that this will upset the productivity or balance of the system to which they belong (Steele in Dyrssen and Jagner 1972; SCEP 1970).

The increased use of concentrated synthetic fertilizers and pesticides has increased agricultural productivity. Although agricultural productivity has increased 50%, use of chemical fertilizers has increased by 300% in certain intensive agriculture areas. It seems we are reaching the point of diminishing returns and these practices need review.

Energy resources are pursued without firm recognition of the exploitation cost. As Rowland (1975) recently pointed out, "What we tend to forget is that energy in the ground is of no use to us until it has been discovered, extracted, processed and delivered, and that all of these procedures consume energy. In the past, our reserves were highly concentrated and easy to get at, but nowadays they are getting more and more inaccessible and we have to divert more and more energy into this energy-getting process. Eventually, a point must be reached where the energy consumed is greater than the energy produced."

Development of the Alberta oil sands may be a case in point. It is proposed to develop the upper Athabasca River for its hydroelectric potential and much of the developed power will be diverted to the oil sands area to satisfy the energy requirements of the new urban areas and the oil extraction plants. Moreover, it appears from preliminary estimates that a good deal of the recovered hydrocarbon will be consumed in the production of synthetic crude oil for the open market. Considering the capital investment required in oil sands, and the losses in converting hydroelectric to electric to petroleum energy, one could speculate that a study should be done on the feasibility of buying each Canadian an electric car. While this proposal may seem facetious, it is made to highlight the fact that basic energy decisions or energetic decisions are seldom considered by governments in situations such as this. When the production of contaminants and their use is added to the picture, one wonders if such major developments are a benefit to Canada.

Although the questions themselves may be spurious in light of political considerations, it would be refreshing to technically and scientifically trained persons if such simple, broad scale matters were considered, researched, and discussed prior to any developments.

The massive area north of 60°N is under development and most observers predict that development will intensify. Much of this development will have chemical and physical impact on arctic waters and on their fisheries resources.

Arctic concerns were also highlighted by Mann (1975) in a study commissioned by FRB. He noted "there is a surprising lack of any program of chemical oceanography in the arctic. Not only is there no program but no one is thinking about one... ." This lack is surprising in view of the Canadian pretense to arctic sovereignty. I would complete Mann's statement "... in Canada, while it is obvious that other countries are quite active through their remote sensing, their navies, and their planning." Dr Mann also noted the tendency to extrapolate data acquired in temperate regions to the

arctic. Such extrapolations may be correct, but this is not known as Canada has little or no arctic research experience in these matters. Our experience with pollutants in arctic marine and fresh waters is minimal, and recently, authorities in Greenland were asked for advice. Thus, Mann's recommendations regarding increased activity in the high arctic marine areas are strongly supported. These activities should be extended to include fresh waters.

It is proposed that Canada convene a series of workshops involving world experts to define problems and nonproblems pertinent to arctic and subarctic development.

Should such meetings be convened, reasoned recommendations should ensue and be published. Too frequently the results of such efforts are buried as dusty government documents, unknown to the public and ignored by the bureaucrats.

A basis for such a meeting might be found in recent efforts by the Freshwater Institute.

In early 1974 the Director of the Institute asked its senior scientist, Dr J. R. Vallentyne, to convene a group to consider strategic guidelines for future northern research to be undertaken by the Institute. The resultant document highlighted several problems which were forcing the Institute into new areas. Specific to this review was the emphasis placed by the group on hydrocarbon exploration and development. The group highlighted five major problem areas which should be of concern to the Institute and it is perhaps worthwhile noting that two dealt with the question of contaminants: 1) petroleum and petroleum products, the effects of oil spills, oil products, and cleanup techniques on northern aquatic ecosystems, and 2) industrial wastes, studies on the response of northern aquatic ecosystems to the addition of mine waste effluents. In their listing of nine separate groups of research topics, I would highlight the listing of: a) petroleum and petroleum products with four major research areas; b) sewage disposal with three major research areas; c) industrial wastes with two major research areas; and d) pesticides and fire retardants with three major research areas, all peculiar to the north. The group highlighted the possibility of thermonuclear wastes in conjunction with any future reactor development north of 60°N.

Public Education

At recent public hearings a citizen made a presentation entitled, "Dilution is not the solution to pollution." In part, the presentation stated that "nothing short of total pollution emission control is acceptable, and that doesn't mean you can throw a little cup of poison in the water, like one pound per year of arsenic in the water. That means none. That's the way it was meant to be and that's the way it should be, ..." (Tapwe J. A. L. Chretian, Giant Yellowknife Mines Hearing, April 22, 1975).

That quote undoubtedly came from the heart, and represents the view of a concerned but relatively uninformed citizen. This is the response of a person who does not understand that total pollution emission control is impossible given the present state of technology. He can only appreciate a portion of the problem.

Any reader of the many publications available on the topic becomes more and more aware of the real lack of any practical ability on our part, either locally, provincially, nationally, or even internationally to reach a truly reasoned decision regarding the use or avoidance of use of a toxicant.

We seem enamored with short-term solutions and avoid the long-term issues. The long-term issues are societal and require political as well as scientific and sociological decisions. The decisions affect the public whose total well-being is very much an issue, whether they know it or not. Consequently, education becomes a key issue.

"Today science affects almost every aspect of our lives, and we can expect this dominance to be even greater in the future. It's thus in the interest of everybody, scientists or not, to gain a better understanding of science and its applications, if only to learn how better to utilize its benefits and to avoid its pitfalls. Such an understanding might be called 'Science literacy'." (Shen 1975.)

A major activity of science to enhance the welfare of man has been to design, synthesize, and apply chemistry (Khan 1973), so it is reasonable to suggest that "science literacy" should have developed quickly in this particular area. However, one questions whether an understanding or "literacy" has developed at all.

It was recently estimated that of the 2 million chemicals synthesized, only about 6000 have ever been tested for carcinogenicity, and only one-half of those were adequately tested (Gillette 1974). Consequently, man seems to be as remarkably careless of his own welfare as of that of the environment on which he is so utterly dependent.

It is widely recognized that use of pesticides is a major factor in the fight to control diseases such as malaria. Increased food production can also be related to pesticide application (Decker 1973). It has been estimated that of the 1.2 billion pounds of pesticides produced in the U.S.,

less than 1% ever hits the target species and, when applied by aircraft, only 25–30% even hits the target area (Pimental and Goodman 1973). Thus, even our technological literacy is in doubt.

The public is aware of the wide-scale use of chemicals novel to the environment, but only recently has concern been expressed regarding the unintended introduction of these materials into the environment. The nearest body of water is still considered a sort of infinite sewer for wastes. Unfortunately, we are now disposing on such a scale and at such a rate that even such "infinite sinks" as the Baltic and Mediterranean seas are in peril and concern is being expressed about the stability of the world ocean itself (SCEP 1970).

However, some sense of "science literacy" may be emerging; there is public concern regarding the "pitfalls" (Shen 1975) of these policies. The increase in the number of learned journalists concerned with pollution is startling as is the increase in articles appearing in the public media. Governments around the world have reacted through the provision of legislation and increased resources.

Canada has followed this pattern and is now investing or planning to invest resources in the solution of these problems. Public investment in research into problems peculiar to the aquatic environment is considerable and apparently growing; it appears appropriate that a course of action be recommended.

The key issue is that the public does not understand or appreciate how and why decisions are reached. To quote Shen (1975):

> "With some over-simplification, the decision-making process in a typical science-related public issue might look something like this. In the first stage, the possible risks or benefits of the proposed action are evaluated, a highly technical process begins with the collection of scientific evidence and ends with the derivation, on the basis of the evidence, of a table of risks and benefits. Then, in the second stage, a policy decision of whether or not to take the action is made on the basis of the risk–benefit table. Such a policy decision requires no technical training.
>
> "One difficulty with science-related issues today is that the layman is often not able to separate the first stage from the second. The situation is not improved when scientists who make pronouncements on public issues do not always bother to point out where science ends and personal opinions begin; and the layman is even more confused when, instead of a single risk–benefit table he finds himself confronted with several contradictory ones, all contending for attention. Whom then is he to believe?"

This situation should be changed without invoking what Shen called science propaganda. It is essential for safety and continuity of the environment to mount a campaign to increase the science literacy of the Canadian public. This campaign must not rely on scientists for they are notoriously unable to communicate with non-scientists. Moreover, I would suggest that it is equally as important to increase the "public literacy" of the Canadian scientist! Indeed, a recent editorial (David 1975) records a call for one-armed scientists because, in the course of recent hearings in the U.S., scientific witnesses insisted on saying, "on one hand, the evidence is so, but on the other hand ..." It is apparent that the typical public service press officer would also be unsatisfactory and probably little more than a source of propaganda.

It is recommended that the scientific education of the public be encouraged by supporting television, radio, films, and authors where emphasis is placed on skill in communication, and not on sensationalism. The decisions regarding toxic chemicals and disposal of effluents are essentially political; to be good, decisions in the long term require a public as well informed as possible. Scientific education of the public is a minor investment of national resources but one that is truly pregnant with return.

Summary

Canada has possibly been successful in avoiding ecological disasters equivalent to those of Japan through luck, dilution, and the intuition of Canadian research and control professionals. Policy makers must realize that the odds of continuing this success are poor. A poker player would predict the chances of continued success as minimal.

Few clear answers to problems posed in this study are readily apparent; however, steps that might be taken by those in authority are suggested. The suggestions can be debated or, at worst, uncritically accepted. This study did not presume to consider human health problems.

Step 1. To review incidents where contaminants have affected commercial or sport fisheries — Placentia Bay, the acid lakes near Sudbury, mercury and PCB's in the Great Lakes basins. The review must define the cost of these incidents to the community, indicate the costs of appropriate control and research programs, and evaluate their utility in mitigating the impact of toxicants. Comparing the economic data of these incidents might suggest cessation of all control and research efforts, but it should not, especially if economics were considered with sociological impacts. This leads to:

Step 2. To establish the sense of commitment to resolve such problems; to develop a sense of budget and policy. Policy is specifically needed but it cannot be elaborated intelligently unless the resultant costs are known to the policy makers. Specific policy issues needing debate or resolution are the depth of public concern (the level of control vs. the attendant cost), the role of government agencies, and the philosophy of the "polluter pays" principle. Given an idea of the consequences and costs of ignoring the problem and some guidance for policy, leads to:

Step 3. To set priorities. What are Canadian interests in these matters? What are the research and control priorities, as Canada cannot afford to assess every problem equally well? New mechanisms for this process will have to be developed. Access to industrial data is essential to the success of any such mechanism. These priorities lead to:

Step 4. To implement research and control programs with close cooperation between departments of federal and provincial governments.

Conclusion: Research and development may prove to be key activities in this area. These activities can be postponed only if increased risk to the populace and to the environment can be accepted.

The risks are posed by an ever increasing use and distribution of toxicants. Can Canada ignore both the good and the bad examples provided by heavily industrialized countries such as England, Germany, and Japan? This is not a plea for unrestricted support of research, but a request that current attitudes be reviewed in light of current problems. Recent public statements by portions of the science community regarding government attitudes and support for science are probably less than useful to elected representatives. What is required is a joint, tightly reasoned approach to cabinet and parliament by all concerned parties.

Acknowledgments

I wish to acknowledge the assistance of Drs A. L. Hamilton, R. R. Wallace, J. F. Klaverkamp, K. Patalas, W. L. Lockhart, and W. G. Franzin who were kind enough to read and comment on drafts of the manuscript. I also wish to acknowledge the contribution of Ms G. Decterow to the format and accuracy of the final typescript.

Mr E. B. Stolee kindly provided major editorial assistance for which I am very grateful.

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Black Bass Biology and Management. *Edited by Henry Clepper. Sport Fishing Institute, Washington, D.C. 1975. x + 534 p. $20 paper, $25 cloth.*

This collection of 54 scientific papers was presented at the First National Bass Symposium, held during 1975, to address concerns about the appropriateness of management procedures for centrarchid bass (genus *Micropterus*). The objectives of the symposium were to critically review current knowledge of the biology and management of bass, to consider current management problems, and to identify management needs in order to direct future research. The papers can be grouped into three sections: 1) reviews of the life history, distribution, taxonomy, behavior, diseases, responses to environmental factors, population dynamics, crops, and species associations of bass; 2) reviews of hatchery culture methods, genetics, stocking, harvest regulations, competitor removal, the use of selective toxicants, artificial reefs, pond fertilization, supplemental feeding, aquatic plant control, and other management techniques in relation to bass; 3) several papers that present results from recent research studies on these topics.

The reviews of bass biology are useful summaries of an enormous amount of literature, but most are not critical evaluations of the present state of knowledge, and future directions for research are seldom discussed. An exception is Eipper's fine review of the interactions between environmental factors, survival of young bass, and year-class strength, although the hypothesis that year-class strength is determined by mortality during the first few weeks should be tested by sequential samples from several populations. Eipper's paper is strengthened by his discussion of the results of other studies on fluctuations in year-class strength, and several reviews, particularly Miller's discussion of comparative behavior, would have benefitted from a consideration of the extensive literature on other centrarchids. I was disappointed by the lack of discussion of the implications of research findings for either theoretical or management problems except in very general terms. I am convinced that although critical reviews are time-consuming and difficult to write, they are essential if fisheries biology is to develop as a science.

The most important problem that confronts managers of freshwater sport fisheries in North America is overexploitation, and the persistent failure of biologists to test hypotheses with experiments and to adequately document management interventions has left managers without a predictive science to lean on. In a brief review of traditional harvest regulations, Fox points out that relatively few efforts have been made to evaluate the effectiveness of the various measures imposed, and the same criticism applies to most of the management methods discussed. Ming and McDannold report on a study, unfortunately terminated prematurely, of the effects of the imposition of a size limit on an overexploited bass population. Dillard and Novinger provide an excellent short review of the wealth of data on stocking of largemouth bass in ponds. Anderson (1973) suggested that this long series of replicated experiments was the basis for the successful management of bass in Alabama ponds, discussed in this book by Smith et al. The models discussed by Anderson and by Lackey et al. should be useful in the continuing search for both biological and political solutions to overexploitation, but an experimental approach to management problems must be developed (Larkin 1972).

This volume will interest those who either manage or do research on centrarchid bass, but will be of limited value to others. The objectives of the symposium were, typically, only partially reached, but the real importance of the symposium may have been the opportunity for discussion between management and research biologists.

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Elements of Oceanography. *J. Michael McCormick and John V. Thiruvathukal. Bibliography and Index. Published by W. B. Saunders Company Canada Limited, Toronto, Ont. 1976. vi + 346 p. $14.95.*

This nicely produced book, printed in light blue on white, provides an excellent text on oceanography: its physical, chemical, and political aspects, is aimed at the "college student as citizen." This is an admirable aim, for at no time has there been a greater need than the present for people generally to have a conscious awareness of the crucial importance of the ocean in relation to the well-being of mankind.

The world ocean, which accounts for two thirds of the earth's solid surface, is now recognized as man's principal resource. It is the earth's great water reservoir — the source of the life-giving atmospheric moisture on which all land plants and animals depend for their development and survival. The waters of the ocean form a huge natural thermostatically controlled heat reservoir which releases heat to the atmosphere in temperate zones in winter thereby alleviating the cold which would otherwise render human life virtually impossible in these regions. The ocean provides for the least expensive mode of transport; it provides a playground for the increasing number of folk who enjoy water sports; its waves and tides have potential value as energy providers for man; the seas provide man with valuable protein from fish and other marine animals; sea water contains in solution an immense store of valuable material; the seabed is the repository of valuable mineral sediments; and the rocks below the seabed are often rich in petroleum, natural gas, sulphur, and other valuable industrial resources. The ocean is also man's principal garbage receptacle; only in recent times are we becoming aware of the dangers which we, and future generations, may have to face, unless greater care is taken in the use of the sea in this role. The oceans, as the authors of this book remark, "are under ever-increasing environmental stress," and they make it clear that the prospects of deriving increased benefit from the seas depend upon human activity and political decisions. Every adult human being, therefore, has a responsibility as a citizen to ensure that wise and sensible decisions relating to the future exploitation of the sea are made.

Sensible decisions stem from adequate knowledge of the factors involved in the matter under consideration. In this respect, this book offers a first-class starting point for any responsibly minded person who wishes to understand the role of the ocean in relation to man's well-being. All the main branches of oceanography are covered in an interesting and easily understood manner, and the work is copiously illustrated with line drawings and photographic reproductions. The brief final chapter deals with "Political Oceanography": here we see the real relevance of the several principles of oceanography which are clearly described and explained in the earlier chapters. The sequential arrangement of the chapters is logical and the book is recommended as a sound elementary text on oceanography and its relevance to people.

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(R119)

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April–May 1976

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(Proceedings of a symposium held in Guelph, Ont., August 14–17, 1972; 78 papers cover evolution, anatomy, behavior, population dynamics, care and management, ecology, physiology, and general topics.)

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(The Board of Associate Editors is issuing individual papers as separates of volumes devoted to particular fields with binding into volumes to be done by subscribers. Speed and economy of publishing are looked for and contributions invited.)

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*To be reviewed.

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Vertical and horizontal distributions of coho salmon (*Oncorhynchus kisutch*), yellow perch (*Perca flavescens*), and cisco (*Coregonus artedii*) in Pallette Lake, Wisconsin **S. Engel and J. J. Magnuson**

Physiological response of juvenile coho salmon (*Oncorhynchus kisutch*) and rainbow trout (*Salmo gairdneri*) to handling and crowding stress in intensive fish culture **G. A. Wedemeyer**

Uptake and retention of Kuwait crude oil and its effects on oxygen uptake by the soft-shell clam, *Mya arenaria* **W. C. Fong**

Visual observations of phosphorus movement between algae, bacteria, and abiotic particles in lake waters **H. W. Paerl and D. R. S. Lean**

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Survival and propensity for homing as affected by presence or absence of locally adapted paternal genes in two transplanted populations of pink salmon (*Oncorhynchus gorbuscha*) **R. A. Bams**

Long-term effects of methylmercuric chloride on three generations of brook trout (*Salvelinus fontinalis*): toxicity, accumulation, distribution, and elimination **J. M. McKim, G. F. Olson, G. S. Holcombe, and E. P. Hunt**

Vertebral number in North American sculpins of the *Myoxocephalus quadricornis*-complex **D. E. McAllister and J. Aniskowicz**

Notholca laurentiae and *N. michiganensis*, new rotifers from the Laurentian Great Lakes region **R. S. Stemberger**

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Inert particle agglutination tests for detection of antibody to enteric redmouth bacterium **C. B. Hansen and A. J. Lingg**

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Flatfish densities determined with a diver-operated flounder sampler **J. M. Walton and N. W. Bartoo**

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Incorporation of fatty acids into phosphatidylcholine by acyl-CoA: 1-acyl-*sn*-glycero-3-phosphorylcholine acyltransferase in liver of rainbow trout, *Salmo gairdneri* **B. J. Holub, J. Piekarski, C. Y. Cho, and S. J. Slinger**

Gonadotropic hormone treatment of rainbow trout (*Salmo gairdneri*). Plasma hormone profile following a single injection **L. W. Crim and D. M. Evans**

Acute toxicity of residual chlorine in wastewater to coho salmon (*Oncorhynchus kisutch*) and some resultant hematologic changes **J. A. Buckley**

Trace metals (As, Cd, Cu, Fe, and Zn) in Arctic cod, *Boreogadus saida*, and selected zooplankton from Strathcona Sound, northern Baffin Island **A. Bohn and R. O. McElroy**

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Manuscript Reports

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tory of Pacific Rim National Park. Fish. Mar. Serv. MS Rep. 1389: 236 p. (1)

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Traductions

Les traductions dont il est question ci-après ont été préparées par ou pour le Service des pêches et des sciences de la mer, à des fins de recherche. On peut en obtenir des exemplaires, à 20¢ la page et à un prix minimum de $2.00 aux Services de traduction, Institut canadien de l'information scientifique et technologique, Conseil national de recherches du Canada, Ottawa (Ontario), K1A 0S2. Le Bureau du rédacteur peut fournir des renseignements sur ces traductions.

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LUKIN, A. V. 1974. Data available on biology of fish in the Volga Cascade reservoirs and areas for further research in the field. Izv. Gos. Nauchno-Issled. Inst. Ozern. Rechn. Rybn. Khoz. 95: 124–128. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3779, 1976)

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DUCET, C., AND G. VANDEWALLE. 1959. New techniques of phosphorus dosage. Ann. Physiol. Veg. 11: 199–205. (Transl. from French by Fish. Mar. Serv. Transl. Ser. No. 3784, 1976)

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List of Establishments

(1) Department of the Environment
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6640 nord-ouest, prom. Marine
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Journal of the Fisheries Research Board of Canada

Guide for Authors

A more detailed guide on preparation of manuscripts from theses is available from the Office of the Editor.

Content

We invite submission of manuscripts in the broad field of fisheries management, ocean science, and aquatic environments relative to Canada.

Articles: Reports of research studies of broad scope that are original contributions to science.

Notes: Differ from papers on the basis of scope or completeness, rather than quality of research. They may be on problems with narrow, readily defined limits; on work that is largely confirmatory; on methodology or research techniques; on advances in knowledge arising as by-products of broader studies; on progress in projects that were discontinued; or on preliminary findings that warrant publication before problems are resolved. They may be organized with as much flexibility as articles except that they have no centered headings and should occupy no more than four printed pages.

Reviews: Detailed articles that are critical appraisals of broad areas of investigation, particularly in fields that have shown rapid development in recent years.

Perspectives: Essays of opinion or hypothesis on fisheries, ocean science, aquatic environments, or related topics that are of concern to the professional and layman. References are desirable; informal style is welcomed.

Letters: Opinion on topics recently under discussion in the *Journal*; preferred maximum length, 500 words. The Editor reserves the right to shorten letters and to make other changes to accord with the style of the *Journal*.

Editorial Practices

The *Style Manual for Biological Journals* (3rd ed. American Institute of Biological Sciences, 3900 Wisconsin Ave. NW., Washington, D.C.) is used as the authority in matters of form. The standards for spelling are: *Webster's Third New International Dictionary* and *le Grand Larousse Encyclopédique*. Titles of periodicals are abbreviated as in the *Biological Abstracts* list. References to literature are made by the name-and-year system. The *Journal* follows the names and spelling recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (3rd ed. 1970) Special Publication No. 6 of the American Fisheries Society.

Series titles should be avoided. An *abstract* is required for all manuscripts, and should state concisely, in less than 250 words, what was done, the essentials of the new knowledge, and the main conclusions. Abstracts are published in English and French; those submitted in one language only are translated by the *Journal*.

The Editor normally submits each manuscript to at least two *referees*. Contributors are encouraged to suggest at least four names to be added to the list from which referees may be selected.

Illustrations should be submitted as photographic reproductions no larger than a standard page and must accompany the manuscript. Prints should not be mounted, stapled, or clipped. Symbols, letters, and numerals must be neat, and at least 1.5 mm high when the illustration is reduced to the appropriate size. Drawings should, when possible, be grouped to facilitate comparisons.

Proofs are sent to the author, who is responsible for correcting only errors in typesetting. *Alterations to the content must be avoided.*

Fifty *reprints* are supplied free. Additional reprints may be purchased at the time of publication (an order form is sent out with the galley proof). All orders should be sent to the Printing Department, University of Toronto Press, 5201 Dufferin Street, Downsview, Ont. M3H 5T8. Invoices relating to the reprints will be sent out by the Printer. A charge of $40.00 per page is made for articles published. When submitting a manuscript, an author should state that his institution will accept this charge.

Checklist on Manuscripts

Attention to the following questions will expedite appraisal of manuscripts by referees and editors.

Are the findings, interpretations, and conclusions adequately documented and relevant to the purpose of the study?

Are all the tables and figures needed, and organized to facilitate comparisons? Are there inconsistencies between tables or figures and the text, or within the text? Should some of the data be made available separately, in a manuscript report or at a data repository? If you use statistical analysis are the statistics subordinate to the research?

Would any of the text be clearer if condensed? Are summary statements given at the beginning of sections and paragraphs, and are details in sections and paragraphs relevant to their topics? Does the organization of the manuscript follow logically from the statement of purpose in the introduction?

Does the *title* encompass the content of the report?

Does the *abstract* give the essentials of the new knowledge?

Is the *introduction* largely limited to the scope, purpose, and rationale of the study? Is review of the literature limited to defining the problem?

Are details of *materials and methods* limited to what scientists need in understanding the design of the study and in judging adequacy of the data?

Are generalizations on the *results* adequate? Are findings distinguished from inferences from them?

Is *discussion* limited to interpretation and significance of the findings?

Journal de l'office des recherches sur les pêcheries du Canada

Guide des Auteurs

On peut se procurer au bureau du Directeur de la publication un guide plus détaillé pour la préparation de manuscrits à partir de thèses.

Sujets

Nous désirons reçevoir des manuscrits s'insérant dans le vaste domaine de la gestion des pêches, des sciences de la mer et des milieux aquatiques au Canada.

Articles: Comptes rendus d'études d'une portée générale, constituant des contributions inédites à la science.

Notes: Se distinguent des articles par la portée et le degré d'achèvement plutôt que par la qualité des recherches. Elles peuvent traiter de problèmes particuliers et bien définis; de travaux qui sont en grande partie confirmatoires; de méthodologie ou de techniques de recherche; de progrès de la connaissance découlant d'études plus vastes; de développements dans des projets abandonnés; ou de découvertes préliminaires qui méritent d'être publiées avant la solution de problèmes à l'étude. Les notes peuvent être présentées d'une façon aussi souple que les articles, mais elles ne doivent pas porter d'en-têtes centrés ni occuper plus de quatre pages.

Critiques: Articles détaillés constituant une appréciation critique de vastes champs de recherches, particulièrement dans les domaines ayant connu de rapides progrès au cours des dernières années.

Perspectives: Essais de l'opinion ou de l'hypothèse sur les pêches, les sciences de la mer, les milieux aquatiques, ou sur des sujets connexes qui intéressent professionnels et profanes. Il est préférable de donner des références et d'écrire, si possible, dans un style simple.

Lettres: Opinions sur des sujets exposés dans le *Journal*. Longueur maximale préférable: 500 mots. Le directeur se réserve le droit de raccourcir les lettres et de faire d'autres modifications dans le style du *Journal*.

Dispositions générales

Le *Style Manual for Biological Journals* (3e éd., publié par l'American Institute of Biological Sciences, 3900 avenue Wisconsin N.O., Washington, D.C.) sert de guide quant à la forme de présentation. Le *Webster's Third New International Dictionary* et le *Grand Larousse Encyclopédique* font autorité pour l'orthographe des mots. Les titres de périodiques sont abrégés suivant les *Biological Abstracts*. Les références bibliographiques dans le texte doivent suivre le système nom de l'auteur-année. Pour les noms de poissons et leur orthographe, le *Journal* suit les recommandations contenues dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (Troisième édition, 1970), Publication spéciale No. 6 de l'American Fisheries Society.

Il faut éviter les *articles en série*. Un *résumé* doit accompagner chaque texte et doit exposer brièvement (moins de 250 mots) le travail accompli, les points essentiels des connaissances acquises et les principales conclusions. Les résumés paraissent en anglais et en français, le *Journal* veillant à la traduction dans le cas des présentations unilingues.

Le directeur soumet d'ordinaire chaque texte à l'approbation de deux *arbitres* ou plus. Nous encourageons les collaborateurs à suggérer au moins quatre personnes dont les noms pourraient figurer sur la liste des arbitres.

Les *illustrations* doivent être sous forme de reproductions photographiques ne pas dépasser les dimensions d'une page normale et accompagner le texte. Elles ne doivent pas être montées, coupées ni brochées. Les symboles, lettres ou chiffres doivent se détacher avec précision et avoir au moins 1,5 mm de hauter lorsque l'illustration est réduite à la grandeur voulue. Les dessins doivent, autant que possible, être groupés pour faciliter l'étude comparative.

L'auteur doit revoir les *épreuves* qu'on lui remet et en corriger seulement les erreurs typographiques. *Il doit éviter de changer le contenu du texte.*

Cinquante *tirés à part* sont fournis gratuitement. Les tirés à part peuvent être achetés au moment de la publication. Un bon de commande à cet effet accompagne les épreuves; il doit être retourné en même temps que celles-ci, non pas au bureau de la rédaction, mais au Printing Department, University of Toronto Press, 5201 Dufferin Street, Downsview, Ont. M3H 5T8, qui se chargera de la facturer. Les frais sont de $40.00 par page pour la publication des articles. Quand un auteur soumet un manuscrit, il doit spécifier que son institution accepte les frais.

Listes de contrôles pour manuscrits

Une attention particulière aux questions suivantes facilitera l'évaluation des manuscrits par les arbitres et les éditeurs.

Les découvertes, interprétations et conclusions sont-elles bien documentées et pertinentes au but de l'étude?

Les tableaux et figures sont-ils tous nécessaires et agencés pour faciliter les comparaisons? Y a-t-il contradiction entre les tableaux ou les figures et le texte, ou dans le texte même? Est-ce que certaines données devraient être présentées séparément, dans un rapport manuscrit ou dans un dépôt de données? Si vous faites une analyse statistique, la statistique cède-t-elle le pas à la biologie?

Le texte y gagnerait-il en clarté s'il était plus condensé, en tout ou en partie? Contient-il des exposés sommaires au début de chaque section ou paragraphe, et les détails de ces sections et paragraphs son-ils pertinents au sujet traité? La marche du manuscrit est-elle conforme à la logique énoncée dans l'introduction?

Le *titre* est-il concis, tout en étant représentatif du contenu du rapport?

Le *résumé* donne-t-il l'essentiel des connaissances nouvelles?

L'*introduction* se limite-t-elle à une esquisse de la portée, du but et des raisons de l'étude? La revue de la littérature se limite-t-elle à la définition du problème?

La section *matériel et méthode* contient-elle le minimum de détails qui permettront aux autres scientifiques de saisir les grandes lignes de l'étude et de juger de la valeur des données?

Les généralisations sur les *résultats* sont-elles adéquates? Permettent-elles de distinguer entre constatations et déductions?

La *discussion* est-elle limitée à l'interprétation et à l'évaluation des découvertes?

Journal of the Fisheries Research Board of Canada

Guide for Typists Preparing Copy

Read "Guide for Authors" in the current volume of the *Journal*. When in doubt about how to type or arrange details, follow *Journal* practice.

Type the manuscript on white bond paper, not flimsy, preferably size 21.5 × 28 cm (8.5 × 11 inches). If possible, use paper with the lines numbered in the margin. Leave all margins at least 2.5 cm wide.

Double-space all parts of the manuscript, including tables, captions for illustrations, footnotes, and the reference list. Underline only material that is to be printed in italics. Indent the first line of each paragraph in the text and of each footnote.

In titles and headings, capitalize the first letter of each word. For small capitals, use small letters.

Indicate all text footnotes by superscript arabic numerals. Number them consecutively throughout the manuscript, starting with those on the title page. Place each footnote immediately below the reference to it, separating it from the text by horizontal lines.

On the first page type only the title, the authors' names and affiliations, related footnotes, and the running head (see Appendix A). Type the abstract on a separate page (see Appendix B). Number all pages, beginning with the title page and including those for tables and captions for illustrations.

Have the author check the finished manuscript, and send the ribbon copy and two other clear copies to the Office of the Editor.

Tables: Examine the current volume of the *Journal* to see how tables are set up (see Appendix C).
Note especially the following concerning *numbered tables:*

Type each on a separate page, using paper without the lines numbered.

Number them with arabic numerals.

Use horizontal lines above and below the headings and below the columns, and seldom elsewhere. Never use vertical lines; leave extra spaces instead.

Indicate table footnotes by superscript small letters and type them below the table.

Place the tables after the list of references.

Where each table is first referred to, type in the margin "Table — near here."

Note that *text tables* are not numbered, are typed with the text, and seldom need horizontal lines (see Appendix C).

Illustrations: Send a photographic reproduction (no larger than 21.5 × 28 cm) of each illustration with the manuscript. Type the author's name and figure number on a strip of paper and fasten it to the back of the print. Do not write or type on the print itself. Also, type the captions in succession on a separate page, headed "Captions for illustrations." Put this page at the end of the manuscript.

Where each figure is first referred to, type in the margin "Fig. — near here."

Mathematical Expressions, Equations, and Formulas: Leave three spaces above and below lines that have much material in superscripts, and above and below equations and formulas. In the various expressions, place each component in its correct position (see Appendix D).

Show all symbols clearly. In the margin, spell out Greek letters the first time they occur, and distinguish between the small letter *l* and the numeral *one*, and between the capital letter *O* and the numeral *zero*. Make other explanatory notes similarly.

References: Check the text to see that all references in the list are referred to. Type the reference list, double-spaced, in the style used in the *Journal* (see Appendix E). Names of journals are abbreviated as in the *Biological Abstracts* list; if an abbreviation is in doubt, type the name in full.

Spellings: About 100 words common in fisheries journals are listed in Appendix F.

Appendices: Appendices A to F are available on request from the Office of the Editor.

Journal de l'office des recherches sur les pêcheries du Canada

Guide pour les secrétaires d'auteurs

Lisez le "Guide des Auteurs" reproduit dans l'édition courante du *Journal*. Si vous avez des doutes sur la façon de dactylographier le texte ou d'en agencer les détails, suivez la pratique du *Journal*.

Dactylographiez le manuscrit sur papier blanc de bonne qualité, et non sur papier pelure, mesurant de préférence 21,5 × 28 cm (8,5 × 11 pouces), laissant toujours une marge d'au moins 2,5 cm. Si possible, employez un papier avec lignes numérotées en marge.

Tout le manuscrit, y compris tableaux, légendes de figures, renvois et références bibliographiques, devra être dactylographié à double interligne. Ne soulignez que les mots qui devront être imprimés en italique. Mettez en retrait la première ligne de chaque paragraphe du texte et de chaque renvoi.

Dans les titres et les en-têtes, n'employez la majuscule que pour le premier mot et les noms propres. Pour les petites majuscules, employez les miniscules du dactylographe.

Indiquez tous les renvois du texte par des chiffres arabes suscrits. Numérotez les renvois consécutivement par tout le texte, à commencer par ceux de la page titre. Placez chaque renvoi directement sous sa référence, le séparant du texte par des lignes horizontales.

La première page ne doit contenir que le titre de la publication, ne nom et l'affiliation des auteurs, les renvois appropriés et le titre courant (voir Appendice A). Dactylographiez le résumé sur une page séparée (voir Appendice B). Numérotez chaque page, à commencer par la page titre, et y compris celles qui contiennent les tableaux et la légende des figures.

Voyez à ce que l'auteur vérifie le manuscrit final, et soumettez la première copie et ainsi que deux copies lisibles au bureau du Directeur de la publication.

Tableaux. Consultez une copie du *Journal* pour la composition des tableaux (voir Appendice C).

Portez une attention particulière à ce qui suit au sujet des *tableaux numérotés*.

Dactylographiez chaque tableau sur feuille séparée, vous servant de papier sans lignes numérotées.

Numérotez les tableaux en chiffres arabes.

Tracez des lignes horizontales au-dessus et au-dessous des en-têtes et au-dessous des colonnes, rarement ailleurs; ne tracez jamais de lignes verticales; laissez plutôt des espaces supplémentaires.

Indiquez les renvois dans les tableaux par les minuscules suscrites et placez les renvois au bas du tableau.

Placez les tableaux à la suite des références bibliographiques.

A l'endroit où le tableau est mentionné pour la première fois, indiquez dans la marge "Tableau — près d'ici."

Remarquez que les *tableaux dans le texte* ne sont pas numérotés, sont dactylographiés avec le texte et ne requièrent que rarement des lignes horizontales (voir Appendice C).

Figures: Envoyez avec le manuscrit un reproduction photographique (21,5 × 28 cm ou moins) pour chaque illustration. Dactylographiez le nom de l'auteur et le numéro de la figure sur une lisière de papier que vous collerez au dos. N'écrivez pas à la main ou à la machine sur la photographie même. En plus, dactylographiez les légendes, dans l'ordre, sur feuille séparée, intitulée "Légendes des figures." Intercalez cette feuille à la suite du texte.

A l'endroit où chaque figure est mentionnée pour la première fois, inscrivez en marge "Fig. — près d'ici."

Equations, formules et expressions mathématiques: Laissez trois espaces au-dessus et au-dessous des lignes renfermant des chiffres ou des lettres suscrits et souscrits, ou encore au-dessus et au-dessous d'équations et de formules. Placez chaque composante des différentes expressions dans la position qui lui est propre (voir Appendice D).

Indiquez clairement tous les symboles. Epelez en marge les lettres grecques, la première fois qu'elles apparaissent. Faites une distinction entre la lettre *l* et le chiffre *un*, et entre la majuscule *O* et le chiffre *zéro*. Insérez de la même façon toute autre note explicative.

Références: Vérifiez le texte afin de vous assurer que toutes les références apparaissant dans la liste bibliographique sont bien mentionnées dans le texte. Dactylographiez à double interligne dans le style en usage dans le *Journal* (voir Appendice E). Les noms de revues sont abrégés suivants les *Biological Abstracts*; en cas de doute, écrivez le nom au long.

Orthographe: Une liste d'environ 100 mots communément employés dans les périodiques sur les pêches est donnée en Appendice F.

Appendices: On peut se procurer une copie des Appendices A à F sur demande au bureau du Directeur de la publication.

Canadian Conference For Fisheries Research

The thirtieth Annual Meeting of the CCFFR will be held at the Lord Beaverbrook Hotel, Fredericton, New Brunswick, January 5 and 6, 1977. The Fisheries Research Board of Canada and the Fisheries and Marine Service, Department of the Environment, will again sponsor this meeting. The President is J. M. Anderson, University of New Brunswick, Federicton, the Secretary is J. C. Stevenson, and the Treasurer is J. Camp, both of the Fisheries and Marine Service, Department of the Environment, Ottawa. Program Chairman is F. W. H. Beamish, University of Guelph, Guelph.

The Canadian Society of Environmental Biologists will also meet at Fredericton, January 4, 1976.

CCFFR Program

Wednesday January 5 0900–1200 h

Contributed Papers Session

Convenor:
P. M. Powles
Department of Biology
Trent University
Peterboro, Ont.

Persons intending to present papers should contact the Convenor at the earliest possible date providing the proposed title and, if possible, an abstract of the paper.

Wednesday January 5 1400–1700 h

Implications of the 200-Mile Zone on
Fisheries Research and Management

Convenor:
A. W. May,
A/Director-General
Resource Services Directorate
Fisheries Management
Ottawa, Ont.

1. Development of a 200-Mile Zone in Law of the Sea
   — Speaker to be confirmed.
2. Management of Pacific Salmon Relative to the 200-Mile zone
   J. MacDonald, Fisheries and Marine Service, Nanaimo, B.C.
3. Atlantic Groundfish Management Relative to the 200-Mile Zone
   L. S. Parsons, Fisheries and Marine Service, Ottawa, Ont.
4. Fisheries Management Concepts and Demands on the Knowledge Base
   B. S. Muir and A. W. May, Fisheries and Marine Service, Ottawa, Ont.

Thursday January 6 0900–1200 h

Changing Patterns of Utilization of Sea Mammals

Convenor:
D. E. Sergeant
Environment Canada
Arctic Biological Station
P.O. Box 400
Ste. Anne de Bellevue, Que.

1. Population Changes in Harp Seals under Exploitation
   D. M. Lavigne, Department of Zoology, University of Guelph, Guelph, Ont.
2. Atlantic Coast Seal Populations and Their Management
   J. Boulva, Laval University, Quebec, Que.
3. West Coast Killer Whales
   M. A. Bigg, Department of the Environment, Pacific Biological Station, Nanaimo, B.C.
4. White Whales in the St. Lawrence; Indirect Effects of Man on Populations
   J. Laurin, Department of Zoology, University of Guelph, Guelph, Ont.

Thursday January 6 1400–1700 h

Embryonic and Larval Periods of Fishes: Present
Status and Significance

Convenor:
E. K. Balon
Department of Zoology
University of Guelph
Guelph, Ont.

A panel discussion with the following members:
D. F. Alderdice*, Department of the Environment, Pacific Biological Station, Nanaimo, B.C.
H. Battle*, Department of Zoology, University of Western Ontario, London, Ont.
D. Faber, National Museums of Canada, Ottawa, Ont.
P. Ihssen, Ontario Ministry of Natural Resources, Maple, Ont.
A. E. Peden*, B.C. Provincial Museum, Victoria, B.C.
C. C. Lindsey, Department of Zoology, University of Manitoba, Winnipeg, Man.

*Not yet confirmed.

Residue dynamics of di-2-ethylhexyl phthalate in fathead minnows (*Pimephales promelas*)
F. L. Mayer 2610–2613
Postmortem bile damage to rainbow trout (*Salmo gairdneri*) livers
J. D. Hendricks, L. J. Hunter, and J. H. Wales 2613–2616
Atlantic salmon (*Salmo salar*) of the Leaf River, Ungava Bay **R. L. G. Lee and G. Power** 2616–2621
Outbreak of infectious pancreatic necrosis in yearling speckled trout (*Salvelinus fontinalis*)
M. A. S. Y. Elazhary, A. Lagace, G. Cousineau, R. S. Roy, L. Berthiaume, P. Paulhus, and J. L. Frechette 2626–2629
Coded spine clipping to identify individuals of the spiny-rayed fish *Tilapia* **J. N. Rinne** 2626–2629
Effects of air-supersaturated water on adult sockeye salmon (*Oncorhynchus nerka*)
A. V. Nebeker, D. G. Stevens, and R. K. Stroud 2629–2633

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Aquatic environmental quality: toxicology **R. D. Hamilton** 2671–2688

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